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Hand-Held-Calculator Programs for the Field Forester

Wayne D. Shepperd

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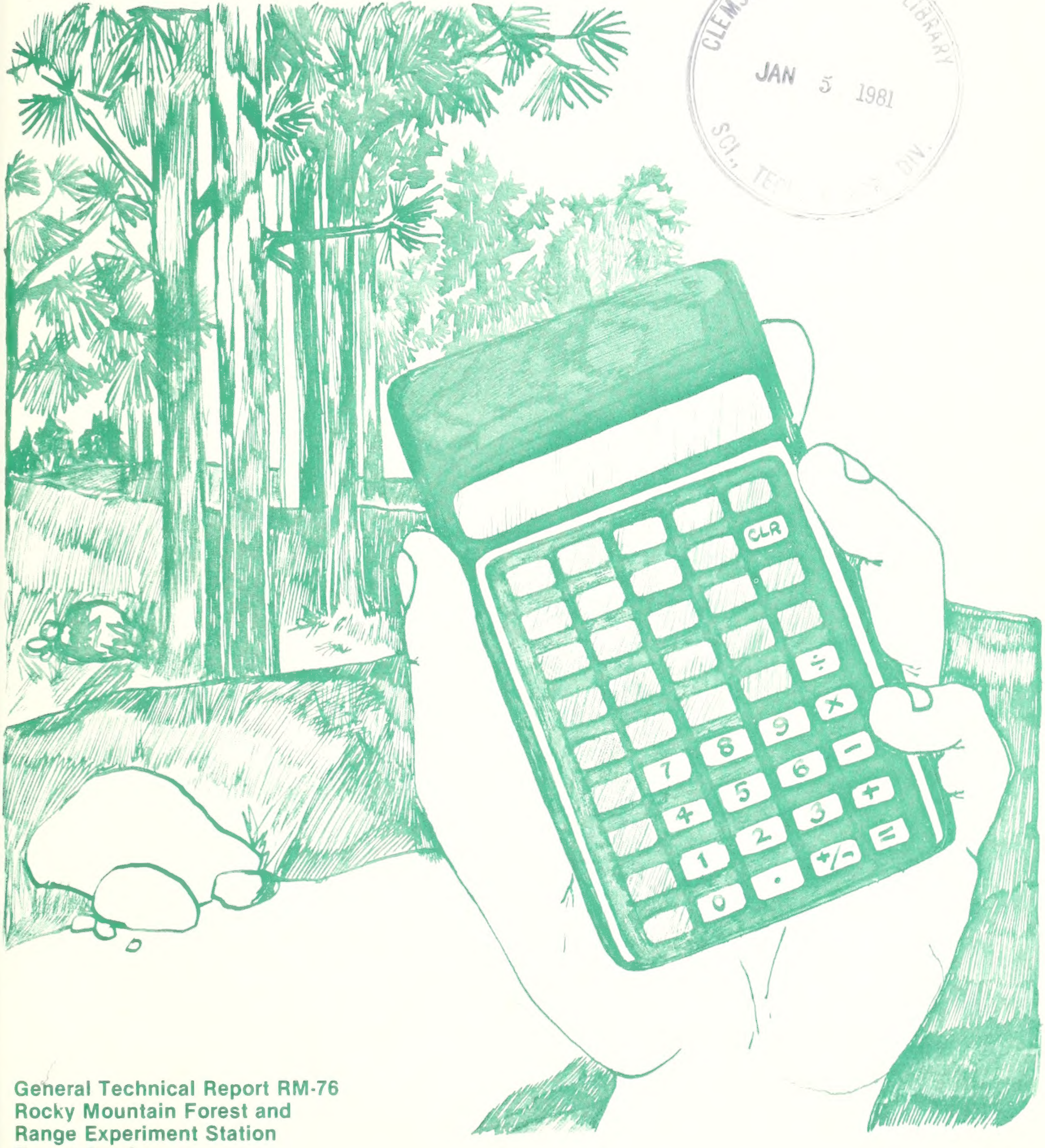

General Technical Report RM-76
Rocky Mountain Forest and
Range Experiment Station
Forest Service
U.S. Department of Agriculture

Abstract

A library of programs written for hand-held, programmable calculators is described which eliminates many of the computations previously done by hand in the field. Programs for scaling aerial photos, variable plot cruising, basal area factor gauge calibration, and volume calculations are included.

Plant a tree! Mark the 75th birthday of the Forest Service by giving a living gift to future generations.

USDA Forest Service
General Technical Report RM-76

July 1980

Hand-Held-Calculator Programs for the Field Forester

Wayne D. Shepperd, Associate Silviculturist
Rocky Mountain Forest and Range Experiment Station[1]

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USDA Forest Service General Technical Report RM-76

Hand-Held-Calculator Programs for the Field Forester
by Wayne D. Shepperd

On page 5, under "Example," the first line should read:

Positive slope percent to tip = 40.

On page 12, under "Formulas Used," second column, first equation should read:

$$\text{acreage} = \frac{(\text{scale of measured area})^2}{6{,}272{,}640} \text{ x photo area in square inches}$$

Hand-Held-Calculator Programs for the Field Forester

Wayne D. Shepperd

Introduction

The increased availability of small, hand-held, programmable calculators has brought the computational power of computers to individual users. These machines offer many advantages. They are small, inexpensive, easy to use, require no special programming skills, and are rugged enough for field use. Newer models store and execute programs containing more than 2,000 steps.

The programs presented here are designed to help the field forester use a programmable calculator to gather and analyze data in field situations. Tedious or complicated math operations are programmed and stored on magnetic cards, which eliminates the need for tables, charts, and reference sources, and reduces computational errors. Knowledge of higher math or programming is not required to run programs.

Foresters working in the field can use these programs to perform calculations used in gathering forest inventory information, estimating tree volumes, and interpreting aerial photos. The amount of time saved by using a programmable calculator can easily pay for it in a short period of time. Calculations which normally require use of large computers, or extensive office computation, can be performed in the field, making the results immediately available.

The programs in this publication are written in outline form and are not specific to any particular brand of calculator. However, a calculator with 200 or more program steps is desirable. The programs are presented in order of complexity, so the user is gradually introduced to more advanced programming techniques.

Calculator Requirements

Several features common to most programmable calculators are necessary to use these programs:

1. User defined keys which execute a series of program steps when pressed.
2. Internal subroutine capability in which a series of program steps are executed when called by a program instruction.
3. Capability of performing trigonometric calculations in the degree mode.
4. At least 20 addressable data memories.
5. Capability of conditional branching (example: IF $a \geq b$ GO TO STEP 24).
6. SET/CLEAR FLAG operations.

Explanation of Terminology

The reader must have a working knowledge of the subject matter and be somewhat familiar with the programming procedures of the calculator to be used. Some terminology and computational techniques used in the program outlines are not identical to those used by calculator manufacturers. An explanation of these follows.

Key.—A user defined function key used to enter data or perform calculations in the proper sequence during program execution. Up to 10 keys labeled **A** through **E** and **A′** through **E′** are used in programs presented here.

Subroutines.—Labeling and calling subroutines differ among machines. Subroutines are labeled numerically here and are called with the command CALL SUBROUTINE xx, where xx is the number of the desired subroutine.

Mathematical computation.—Notation and hierarchies differ. Algebraic notation is used here, and parentheses or equal signs are used for clarification.

Memory register operations.—Again, commands differ. In this paper, SUM 01 means add the product of the preceding program step to memory 01. STORE 02 means store the product of the preceding program step **in place of** whatever was in memory 02. RECALL 03 brings the contents of register 03 into the display register.

Program control statements.—All programs assume execution of programmed operations will begin when a user defined key or a RUN key is pressed, and will continue until a STOP statement or the end of program memory is encountered. RETURN is used to continue execution after a subroutine. The next step processed is the one following the statement containing the CALL

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SUBROUTINE xx command. CHANGE SIGN commands the calculator to change the algebraic sign of the number in the display register. Conditional branching operations are listed as IF statements. For example, IF $a \geq b$ GO TO 120. This means that, if **a** is greater than or equal to **b**, go to step 120, otherwise continue with the next step. The INITIALIZE PROGRAM instruction at the beginning of most program outlines can be a part of the program or done manually just prior to program execution. All data registers and flags should be cleared, and the program pointer reset to step 0 in this operation.

More efficient programming techniques could have been used in programs presented here, but in the interest of clarity and universal application, they were structured for easy translation. Most of the programs can easily be adapted for use on smaller machines, since they were written using a format, which allows programs to be subdivided into two or more programs to fit machines with smaller program memories.

In addition to a program outline, examples are provided to help correct mistakes when the programs are first put into the calculator. The formulas used in each program are included along with an explanation of the calculations performed in each subroutine. These will also aid in transferring the programs to other machines, or making modifications to fit a user's local needs. Operating instructions are given with each program to aid future nonprogramming users.

Slope to Horizontal Distance

This program converts slope distance to horizontal distance and computes the vertical rise. Data entry can be slope distance, in meters, chains, or feet, and decimal degree angle, topographic angle, or percent slope. Output distances will be in the same form as input distances.

Formulas Used

Assuming that the slope angle will vary from 0° to 90°, percent slope can be converted to degrees as follows:

$$\text{Arctan}\left(\frac{\%\text{ slope}}{100}\right) = \text{degree slope angle}$$

Topographic (1:66) slope angle also can be converted to degrees using the same relationship:

$$\text{Arctan}\left(\frac{\text{Topo. slope}}{66}\right) = \text{degree slope angle}$$

Knowing the degree slope angle, slope distance can be converted to horizontal distance by:

$$\cos(\text{degree slope angle}) \times \text{slope distance} = \text{horizontal distance}$$

Vertical rise can then be obtained by:

$$(\text{horizontal distance}) \times \tan(\text{degree slope angle}) = \text{vertical rise}$$

Program Description

User defined keys perform the following functions:

A Stores slope distance.
B Inputs and stores degree slope angle.
C Inputs percent slope angle; computes and stores degree slope angle.
D Inputs topographic slope angle; computes and stores degree slope angle.
E Computes horizontal distance and vertical rise.

User Instructions

1. Initialize program.
2. Enter slope distance, press **A**.
3. Enter degree slope angle, press **B**.
   or, Enter percent slope, press **C**.
   or, Enter topographic slope angle, press **D**.
4. Press **E**, observe horizontal distance.
5. Press **RUN**, observe vertical rise.
6. Go to step 2 and repeat if desired.

Example

For a slope distance of 100:

Slope angle	Horizontal distance	Vertical rise
10°	98.48	17.36
10%	99.50	9.95
10 topo.	98.87	14.98

Program Outline

Key	Description
A	Enter slope distance STORE 01 STOP
B	Enter degree slope angle STORE 02 STOP

C Enter percent slope angle, compute degree angle

$$\text{Arctan}\left(\frac{\%\ \text{slope}}{100}\right) = \text{degrees}$$

STORE 02
STOP

D Enter topographic (1:66) slope angle, compute degree angle

$$\text{Arctan}\left(\frac{\text{topo. slope}}{66}\right) = \text{degree angle}$$

STORE 02
STOP

E Compute horizontal distance and vertical rise
cos (RECALL 02) x RECALL 01 =
STOP
x tan (RECALL 02) =
STOP

Data Registers Used

01 = Slope distance
02 = Slope angle in degrees

Basal Area Computation

This program is designed to provide either field or office computation of basal area (BA), in square feet, given tree diameters at breast height (d.b.h.), in inches and tenths. To avoid repetitive entering of the decimal point, d.b.h. x 10 may also be entered. Results computed are: total BA of all d.b.h.'s entered, and average d.b.h. (figured from the average BA). A basal area also may be entered, and the machine will calculate the d.b.h of that BA. To be compatible with tables and other computer calculated basal areas, the following formula was used.

$$\text{BA} = \text{d.b.h.}^2 \times 0.005454$$

Program Description

After each tree diameter has been entered using key **A** or **B**, subroutine 01 is called to calculate the basal area, sum the result in an accumulator register, and increment a counter by one. Key **C** recalls the accumulated basal area. Key **D** calculates the average d.b.h. from the average basal area using the formula:

$$\text{Average d.b.h.} = \sqrt{\frac{\frac{\Sigma\text{BA}}{n}}{0.005454}}$$

User Instructions

1. Initialize program.
2. Enter d.b.h., push **A**, or enter d.b.h. x 10, push **B** (display shows BA). After all d.b.h.'s are entered:
3. Push **C** for total BA.
4. Push **D** for average d.b.h. Note: More d.b.h.'s can be entered, after pushing **C** and **D**, if desired.
5. For a new set of d.b.h.'s, go to step 1 and repeat. To find out how many d.b.h.'s have been entered, push **RCL** 02.

Example

d.b.h.	BA
10.2	0.5674
11.5	0.7213
12.6	0.8659
9.5	0.4922
Total BA	= 2.6468
Average d.b.h.	= 11.0148

Program Outline

Key	Description
	INITIALIZE PROGRAM
A	Enter d.b.h. CALL SUBROUTINE 01 STOP
SUBROUTINE 01	Calculate BA $\text{d.b.h.}^2 \times 0.005454 = \text{BA}$ STORE 03 SUM 01 1 SUM 02 RECALL 03 RETURN
B	Enter d.b.h. x 10 $\frac{\text{d.b.h.} \times 10}{10} = \text{d.b.h.}$ CALL SUBROUTINE 01 STOP
C	Display total BA RECALL 01 STOP

D Calculate average d.b.h.

$$\frac{\frac{\text{RECALL 01}}{\text{RECALL 02}}}{0.005454} = \text{d.b.h.}^2$$

$\sqrt{\text{d.b.h.}^2}$

STOP

Data Registers Used

01 = BA sum

02 = Number of entries

03 = Individual tree BA

Tree Heights

This program allows easy field computation of tree heights where adjustments in calculations are necessary because of steep slopes, positive base angles, or conditions that prohibit sighting a tree from standard slope distances.

Program Description

Slope percent clinometer readings are entered in routines **A**, **B**, and **B′** and converted to degree angles using the following formula:

$$\text{Arctan}\left(\frac{\%\ \text{slope}}{100}\right) = \text{degree slope}$$

An angle is considered negative when the base of the tree is below a horizontal line from the viewer to the tree (fig. 1). When the tree base is above this line, the angle is considered positive (fig. 2). Both negative and positive angles to the base of the tree may be entered.

In both cases, **A** is equal to 90° minus $\mathbf{B}_1$, and the height of the tree (**b**) is calculated in subroutine C by:

$$b = \frac{a \sin B}{\sin A}$$

where **a** is the distance from the viewer to the tree base. The slope to the base of the tree is limited only by the capability of the instrument, since slope adjustment tables are unnecessary. The program can be modified for use with a topographic (1:66) scaled clinometer or abney level by changing the constant in the percent slope conversion formula from 100 to 066.

User Instructions

1. Initialize program.
2. Enter slope percent to tip, press **A**.
3. Enter slope percent to base.
   If positive, press **B′**.
   If negative press **B**.
4. Enter slope distance to base of tree, press **C**.
5. Observe tree height.
6. Go to step 1 and repeat as needed.

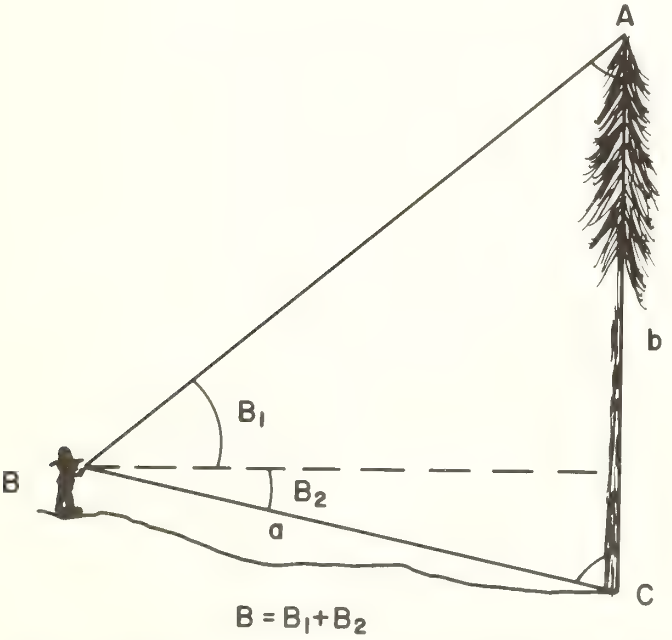

Figure 1.—Measuring tree heights where a negative base angle (B_2) occurs.

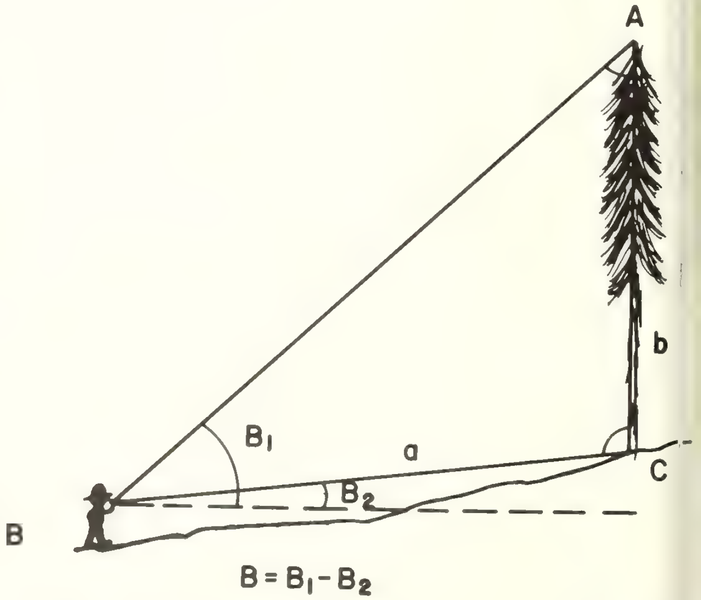

Figure 2.—Measuring tree heights where a positive base angle (B_2) occurs.

Example

Positive slope percent to base = 40.
Negative slope percent to base = 20.
Distance to tree = 56.
Computed height = 32.9
Positive slope percent to tip = 40.
Positive slope percent to base = 20.
Distance to tree = 56.
Computed height = 10.9

Program Outline

Key **Description**

INITIALIZE PROGRAM

A Enter slope percent to tip (B_1)

$$\text{Arctan}\left(\frac{B_1}{100}\right) = B_1 \text{ in degrees}$$

STORE 01
STOP

B Enter negative percent slope to base (B_2)

$$\text{Arctan}\left(\frac{B_2}{100}\right) = B_2 \text{ in degrees}$$

B_2 + RECALL 01 = B
STORE 02
STOP

B′ Enter positive percent slope to base (B_2)

$$\text{Arctan}\left(\frac{B_2}{100}\right) = B_2 \text{ in degrees}$$

B_2 − RECALL 01 = −B
CHANGE SIGN
STORE 02
STOP

C Enter slope distance (a); calculate tree height

$$\frac{a\,(\sin(\text{RECALL } 02))}{\sin(90 - \text{RECALL } 01)} = \text{tree height}$$

STOP

Data Registers Used

01 = B_1

02 = B

Adequacy of Sample Test

This program allows the user to enter a set of data values and test for the size of sample needed to adequately estimate the population variation at a given confidence level. It is very useful in a field situation to check to see if a sample of adequate size has been taken before leaving the site.

Formulas Used

Snedecor and Cochran (1967) give the following formula for determining the number of samples needed, based on preliminary sample data:

$$N = \frac{4\hat{\sigma}^2}{L^2}$$

where:

N = estimated sample size needed
$\hat{\sigma}^2$ = variance of preliminary sample
L = allowable error of the sample mean in sample units. In this program, L is expressed as a proportion of the mean

The variance of the preliminary sample data is calculated using the following formula:

$$\hat{\sigma}^2 = \frac{\sum_{i=1}^{n} X_i^2 - \dfrac{\left(\sum_{i=1}^{n} X_i\right)^2}{n}}{n-1} = \frac{\sum_{i=1}^{n} X_i^2 - n\bar{X}^2}{n-1}$$

where **n** is equal to the size of the preliminary sample. This formula is based on a 95% level of confidence, which means that there is a 5% chance that the population mean will exceed the allowable error limit (L) when a sample of size N is taken.

Program Description

A Enters sample data and accumulates statistical data for sum, mean, and variance.

B Prints and labels number of data points entered and sum.

C Prints and labels mean.

D Calculates, prints, and labels variance.

E Enters allowable error, and calculates the sample size needed to be within that error limit. Labels and prints the results.

User Instructions

1. Initialize program.
2. Enter data value, press **A**.
3. Repeat step 2 until all data values are entered.
4. Press **B** to calculate sum.
5. Press **C** to calculate mean.
6. Press **D** to calculate variance.
7. Enter the allowable error desired as a percent of the mean (e.g., enter 0.05 = ± proportion of mean allowed). Press **E** to calculate the sample size needed to satisfy the allowable error.
8. Repeat step 7 if desired.
9. Go to step 1 to enter another set of data.

If the preliminary sample is inadequate to meet the allowable error, take additional observations and retest for adequacy.

Example

Preliminary Observations

10.
20.
15.
18.
12.
14.
18.
12.
14.
14.
16.
10.

Number of observations =	12.	= n
Sum =	173.	= Σ
Mean =	14.4	= $\bar{X}$
Variance =	10.0	= S^2
Allowable error =	0.05	
Sample size needed =	77.6	= N

Based on the preliminary observations, 78 observations are needed to adequately sample the population at a 5% confidence level.

Program Outline

Key	Description
	INITIALIZE PROGRAM
A	Enter X_i SUM 01 X^2 SUM 02 1 SUM 03 STOP
B	Calculate sum RECALL 01 STOP
C	Calculate mean $\frac{\text{RECALL 01}}{\text{RECALL 03}} =$ STORE 04 STOP
D	Calculate variance $\frac{(\text{RECALL 02}) - (\text{RECALL 03}) \times (\text{RECALL 04})^2}{(\text{RECALL 03}) - 1} =$ STORE 05 STOP
E	Enter allowable error and calculate samples needed STORE 06 $\frac{4 \times \text{RECALL 05}}{(\text{RECALL 04} \times \text{RECALL 06})^2} =$ STOP

Data Registers Used

01 = Sum
02 = Sums of squares
03 = Number of data values
04 = Mean
05 = Variance
06 = Allowable error

Multispecies Board Foot Volumes

This program calculates board foot volumes for Engelmann spruce, lodgepole pine, ponderosa pine, and aspen. All volumes are Scribner board foot to a 6-inch top. Regression equations used to calculate volumes come from volume tables developed for the Rocky Mountains by Peterson (1961), Myers (1969), Myers and Edminster (1972), and Edminster et al. (1980). The ponderosa pine equations are for the Front Range of Colorado only. Predicted volumes generally are very good over the range of the data used to develop the regressions; however, forest specific volume tables may be more accurate locally. The intention of this program is to give foresters a means of obtaining a quick, field estimate of volumes without having to calculate manually from volume tables.

Program Description

Regression equations for Englemann spruce, lodgepole pine, and ponderosa pine take the form:

$$\text{Vol.} = a + b\,D^2H$$

where:

D = d.b.h. outside bark (in inches)
H = total height (in feet)
a,b = regression constants

In practice, two equations are used for each of the above species—one for D^2H values below a certain limit, the other for D^2H values above that limit. Regression constants and D^2H limits for the conifer species are listed below:

Engelmann spruce
  For D^2H to 12,200
    $a = -15.14466$
    $b = 0.01097$
  For D^2H larger than 12,200
    $a = -27.91343$
    $b = 0.01202$

Lodgepole pine
  For D^2H to 22,800
    $a = -6.00933$
    $b = 0.01202$
  For D^2H larger than 22,800
    $a = -19.76641$
    $b = 0.01263$

Ponderosa pine
  For D^2H to 2,830
    Volume = 8
  For D^2H larger than 2,830
    $a = -24.5404$
    $b = 0.01149$

When d.b.h. and height are entered and one of the above species' subroutines is called, by pressing **C**, **D**, or **E**, the program:

- calculates D^2H
- tests the D^2H limit for that species
- calls subroutine 01 which then calculates the volume
- stores the volume in a species total register and a grand total register
- displays the tree volume by species.

For aspen, a single logarithmic regression equation is used (Peterson 1961):

$$Y = 1.1214X_1 + 0.9427X_2 - 1.9840$$

where:

$Y = \text{Log}_{10}$ (volume to 6-inch top inside bark – 9)
$X_1 = \text{Log}_{10}$ [(d.b.h. inside bark)^2 + 36]
$X_2 = \text{Log}_{10}$ (height to 6-inch top inside bark – 8.15)
d.b.h. inside bark = 0.8954 d.b.h. outside bark + 0.3168.

When the d.b.h. and **height to a 6-inch top** are entered and the aspen subroutine is called, by pressing **E′**, the d.b.h. and height are processed directly through this routine to yield the volume.

User Instructions

If d.b.h. data will be entered from a tally sheet by diameter classes with a 0.5 midpoint (e.g., 14-inch class = 14.0 inches – 14.9 inches), press **A′**. Otherwise, enter the actual measured d.b.h. of each tree.

1. Enter d.b.h. (e.g., 8.5 or 8 if **A′** was pushed), press **A**.
2. Enter height, press **B**. Enter total tree height for all species except aspen. Enter height to a 6-inch top for aspen.
3. Press species key desired:

   C = Engelmann spruce
   D = Lodgepole pine
   E = Front Range ponderosa pine
   E′ = Aspen

4. Record volume.
5. Repeat steps 1-4 until all trees have been entered.
6. Press **B′** for grand total of all species entered.
7. Press **C′** for Engelmann spruce total volume; then, press RUN for lodgepole pine total, press RUN for ponderosa pine total, press RUN for aspen total.

Example

Results if a 10.5 d.b.h., 50-foot tree is entered for each species:

Volume	Species
45.	Spruce
60.	Lodgepole
25.	Ponderosa
91.	Aspen
222.	Total board feet

Program Outline

```
Key             Description

                INITIALIZE PROGRAM

A               Enter d.b.h.
                 + RECALL 11 =
                STORE 01
                STOP

A′              Set d.b.h. class midpoint
                0.5
                STORE 11

B               Enter height, and calculate D$^2$H
                STORE 02
                x (RECALL 01)$^2$ =
                STORE 03
                STOP

Enter species

C               Engelmann spruce
                IF RECALL 03 $\geq$ 12,200:
                 0.01202 STORE 04
                 27.91343 STORE 05
                otherwise:
                 0.01097 STORE 04
                 15.14466 STORE 05
                CALL SUBROUTINE 01
                SUM 06
                SUM 10

SUBROUTINE 01   Calculate conifer volumes
                RECALL 04 x RECALL 03
                  – RECALL 05 =
                RETURN

D               Lodgepole pine
                IF RECALL 03 $\geq$ 22,800:
                  0.01263 STORE 04
                  19.76641 STORE 05
                otherwise:
                  0.01202 STORE 04
                  6.00933 STORE 05
                CALL SUBROUTINE 01
                SUM 07
                SUM 10
                STOP

E               Front Range ponderosa pine
                IF RECALL 03 $\leq$ 2,800:
                  8
                  SUM 08
                  SUM 10
                  STOP
                otherwise:
                  0.01149 STORE 04
                  24.5404 STORE 05
                CALL SUBROUTINE 01
                SUM 08
                SUM 10
                STOP

E′              Aspen
                (RECALL 01 x 0.8954 + 0.3168)$^2$
                   + 36 =
                Log$_{10}$
                x 1.1214 =
                STORE 12
                RECALL 02 – 8.15 =
                Log$_{10}$
                x   0.9427 – 1.9840 + RECALL 12
                Antilog$_{10}$, or $10^x$ =
                 + 9 =
                SUM 09
                SUM 10

B′              Display total volume
                RECALL 10
                STOP

C′              Display species total
                RECALL 06
                STOP

RUN             RECALL 07
                STOP

RUN             RECALL 08
                STOP

RUN             RECALL 09
                STOP
```

Data Registers Used

01 = d.b.h.
02 = Height
03 = D^{2}H
04 = b, regression function
05 = a, regression function
06 = Engelmann spruce volume total
07 = Lodgepole pine volume total
08 = Ponderosa pine volume total
09 = Aspen volume total
10 = Grand total volume
11 = 0.5 for d.b.h. midpoint
12 = Temporary aspen calculation

BAF Gauge Calibration

This program enables the user to calibrate or construct an angle gauge for variable plot cruising using any basal area factor (BAF). If any two of the following variables are known, the program will calculate the third: (1) BAF, (2) width of cruising gauge, or (3) sighting distance (distance from eye to gauge).

A wedge of known width can be converted to any BAF simply by computing the distance it is held from the eye and placing knots in the cord denoting each distance. Existing gauges can be calibrated and checked for accuracy. Or if desired, the BAF of one's thumb can be determined eliminating the need for a gauge.

Formulas Used

The BAF for basal area in square feet per acre can be found using the following formula (Husch 1963):

$$BAF = 43{,}560 \times \sin^2\Theta/2$$

where:

Θ = angle covered by the gauge when viewed at a given distance.

The trigonometric model in figure 3 applies.
Angle A can be determined from the BAF formula as follows:

$$BAF = 43{,}560 \times \sin^2 A$$

$$\sin A = \sqrt{\frac{BAF}{43{,}560}}$$

$$A = \text{Arc sin} \sqrt{\frac{BAF}{43{,}560}}$$

Right triangle solutions for a and b are:

$$A = \frac{a}{\tan A} = \text{sighting distance}$$

$$a = b \tan A$$
$$2a = \text{width of angle gauge}$$

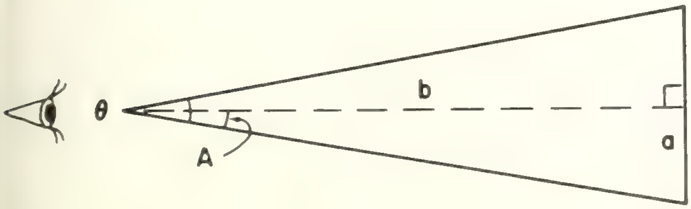

Figure 3.—Trigonometric model for basal area factor gauge calibration.

If BAF is not known, A is found by

$$\frac{a}{b} = \tan A$$

$$A = \text{Arctan} \left(\frac{a}{b}\right)$$

Program Description

User defined keys **A, B,** and **C** are used to enter and store BAF, gauge width, and sighting distance, respectively. Flags are set when each of these variables are entered. Pressing **A′** calculates BAF, given sighting distance and gauge width. **B′** calculates gauge width given BAF and sighting distance. **C′** calculates sighting distance given BAF and gauge width. Set flag tests will not allow computation of any of these variables if the proper data has not been entered. Internal subroutine 02 is called by **B** and **C** to calculate angle A. Subroutine 01 is called to flash the display if the necessary data have not been entered.

User Instructions

1. Initialize program
2. Enter **any two** of the following:
   a. BAF, press **A**.
   b. Gauge width, press **B**.
   c. Sighting distance, press **C**.
3. Press **A′** to compute BAF.
   B′ to compute gauge width.
   C′ to compute sighting distance.
4. Go to 2 and repeat as needed.

Example

BAF = 10
Gauge width = 0.75 inch
String length = 24.75 inches

Program Outline

Key	Description
	INITIALIZE PROGRAM
A	Enter BAF STORE 01 SET FLAG 01 STOP
B	Enter gauge width ÷ 2 = STORE 02 SET FLAG 02 STOP

```
C                Enter string length
                 STORE 03
                 SET FLAG 03
                 STOP

A′               Calculate BAF
                 IF FLAG 02 is not set:
                   CALL SUBROUTINE 01
                 IF FLAG 03 is not set:
                   CALL SUBROUTINE 01
                 $[\sin [\text{Arctan} \left(\frac{\text{RECALL 02}}{\text{RECALL 03}}\right)]]^2$
                   x 43,560 =
                 STOP

SUBROUTINE 01    Indicate error by flashing
                   display
                 $\sqrt{-1}$
                 STOP

B′               Calculate gauge width
                 IF FLAG 01 is not set:
                   CALL SUBROUTINE 01
                 IF FLAG 03 is not set:
                   CALL SUBROUTINE 01
                 CALL SUBROUTINE 02
                   RECALL 03 x tan (RECALL 04)
                     x 2 =
                 STOP

SUBROUTINE 02
                 $\text{Arc sin} \sqrt{\frac{\text{RECALL 01}}{43{,}560}} =$

                 STORE 04
                 RETURN

C′               Calculate string length
                 IF FLAG 01 is not set:
                   CALL SUBROUTINE 01
                 IF FLAG 02 is not set:
                   CALL SUBROUTINE 01
                 CALL SUBROUTINE 02

                 $\frac{\text{RECALL 02}}{\tan(\text{RECALL 04})} =$

                 STOP
```

Data Registers Used

01 = BAF
02 = Gauge width x 2
03 = String length
04 = Angle A

Limiting Distance

This program calculates the limiting distance from plot center to a tree of any d.b.h. in a variable-radius cruise plot. It is especially useful when a precise determination is needed for trees not easily seen with a prism or cruising wedge, or if adjustments for steep slopes are necessary.

If a tree appears to be borderline (i.e., it is hard to tell if the tree is in or out of the plot using a BAF gauge or prism), the user proceeds as follows:

1. Measure the d.b.h. of the tree in question.
2. Measure the distance from the center of the tree to the plot center (SD) as shown in figure 4.

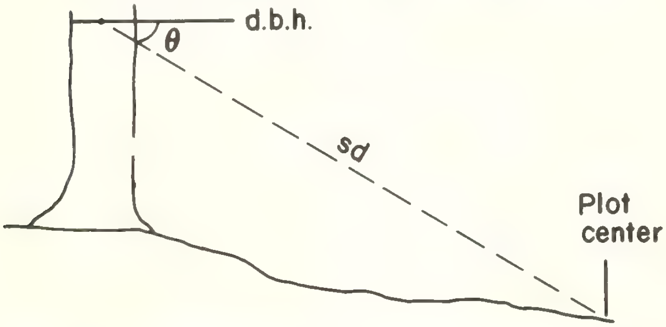

Figure 4.—Measuring the distance from the center of the tree to plot center.

3. Measure the slope from the center of the tree to plot center (angle Θ) in degrees or percent.

4. Using this information, the calculator will compute the limiting distance for a tree of the measured d.b.h., compute the actual horizonta distance from the center of the tree to plot center and determine whether the tree is "in" or "out" of the variable radius plot.

Formulas Used

In a variable radius plot, the plot radius is dependent upon the diameter of each tree to be measured. The d.b.h. of a tree multiplied by a plot radius factor for a given BAF gives the limiting distance or plot radius for that d.b.h. Any tree of the same d.b.h. located beyond this distance from the plot center is considered out and should not be measured. A regression analysis was performed on plot radius and basal area factors listed by Dilworth and Bell (1971) to obtain the following relationships:

$$\text{Plot radius factor} = \sqrt{\frac{1}{y}}$$

when $y = 0.0132232494 \times \text{BAF}$.

Program Description

This predicts the plot radius factor for a given BAF, in key **A**. The plot radius factor is multiplied by d.b.h. in key **B** to obtain limiting distance.

Actual slope distance is input using key **C** and, given the angle of slope, (Θ) used in **D** to calculate the actual horizontal distance as follows:

$$\cos \Theta \times \text{slope distance} = \text{horizontal distance}$$

Percent slope input using key **D′** is converted to a degree angle before being processed in the above formula.

Key **E** determines whether a tree is in or out of the plot by algebraically subtracting actual horizontal distance from limiting distance and attempting to take the square root of the result. If the result is negative (i.e., the tree is "out"), the routine is aborted and the display flashes. If the tree is "in," the routine completes, and the distance by which the tree is inside the plot is shown.

This computational technique not only adjusts for slope, but also accounts for leaning or crooked trees because limiting distance is assumed to be the horizontal distance from the center of the tree at d.b.h. to the plot center.

User Instructions

1. Initialize program.
2. Enter BAF, press **A**, observe plot radius factor.
3. Enter d.b.h., press **B**, observe limiting distance.
4. Enter measured slope distance (SD), press **C**.
5. Enter slope angle (Θ):
   if in degrees, press **D**.
   if in percent slope, press **D′**.
   observe actual horizontal distance.
6. Press **E**. If the display flashes, the tree is "out" and not tallied. If tree is "in," the display will indicate the distance the tree is inside the limit.

Example

BAF = 40
d.b.h. = 12.5 inches
Computed limiting distance = 17.19 feet
Slope distance = 18.0 feet
Slope = 30% or 16.7°
Computed horizontal distance = 17.24 feet
Tree is "out" by 0.05 foot

Program Outline

Key	Description
	INITIALIZE PROGRAM
A	Enter BAF, calculate plot radius factor $\sqrt{\dfrac{1}{BAF \times 0.0132232494}} =$ STORE 01 STOP
B	Enter d.b.h., calculate limiting distance d.b.h. x RECALL 01 = STORE 02 STOP
C	Enter slope distance STORE 03 STOP
D	Enter slope in degrees, calculate horizontal distance COS (slope in degrees) x RECALL 03 = STORE 04 STOP
D′	Enter percent slope, calculate horizontal distance $\text{Arctan}\left(\dfrac{\%\ \text{slope}}{100}\right) =$ GO TO D STOP
E	Determine if the tree is in or out RECALL 02 – RECALL 04 = X $\sqrt{X}$ X^2 STOP

Data Registers Used

01 = Plot radius factor
02 = Limiting distance
03 = Slope distance
04 = Actual horizontal distance

Photo Work Program

This program[2] performs all calculations necessary to determine photo scales, stand scales, and stand acreages for inventory and sale layout work, using U.S. Geological Survey topographic maps, aerial photos, and dot grids or planimeter.

Distances are measured between two points at the same elevation using both the map and the photo. The program calculates a photo scale at that elevation and automatically adjusts it to a prescribed standard elevation for the effective area of the photo.

Once enough measurements have been taken to establish a reliable photo scale, the program can compute acreages for any portion of a photo's effective area. A planimeter reading or dot count is input along with the photo scale, photo scale elevation, and the mean elevation of the measured area. The program computes an adjusted scale for the measured area and uses it to determine the acreage.

Formulas Used

A photo scale at elevation A is computed by:

$$\frac{\mathrm{MD}}{\mathrm{PD}} \times \mathrm{MSF} = \text{calculated scale}$$

where:

MD = Distance between two points at elevation A measured on a map

PD = Distance between the same two points measured on a photo

MSF = Map scale factor = $\frac{1}{\text{map scale}}$

(e.g., a topographic map with a scale of 1/24,000 would have a MSF = 24,000)

This computed scale at elevation A can be adjusted to a standard elevation B as follows:

$$(B - A) \times K = \text{change in scale}$$

This can be a positive or negative change.

K = scale change factor which is dependent upon the focal length of the lens used in the aerial photography and is calculated by:[3]

$$K = \frac{12}{\text{focal length of lens in inches}}$$

The change in scale is algebraically added to the calculated scale to obtain the adjusted scale at elevation B.

Once a standard photo scale at elevation B has been determined, acreages of a portion of the photo at any elevation can be calculated. First, a scale for area to be measured is calculated by adjusting the standard scale to the average elevation of the area to be measured. This scale is then multiplied by the area (in square inches) measured on the photo to obtain the number of square inches represented on the ground by the measured area. The result is then divided by the number of square inches in an acre to get the acreage of the area. Therefore:

$$\text{acreage} = \frac{\text{photo area in square inches x scale of measured area}}{6{,}272{,}640}$$

Program Description

This program is essentially two programs in one. The first enables the user to determine a standard photo scale at a given elevation. The second calculates the acreage of an area measured on a photo of known scale.

User defined keys are used as follows:

A Initializes program and stores a map scale of 1:24,000.

A′ Initializes program and stores a map scale of 1:62,500.

B Stores a distance measured between two points on a map.

C Inputs the measured distance between the same two points on a photo, and calculates a scale.

D Stores the elevation of the measured points.

D′ Stores the desired standard elevation for the photo scale and adjusts the scale computed in C to the standard elevation.

B′ Stores photo scale and photo scale elevation.

E Inputs dot count from a dot grid with 64 dots per square inch and converts to square inches. Inputs elevation of measured area and computes scale and acreage.

This program uses a scale change factor of 1.46 per foot of elevational change. This assumes that a camera with a lens focal length of 8.21 inches was used in the aerial photography. Program steps containing the scale change factor will need to be changed if other focal length lenses are used. Again, scale change factors for other focal lengths may be calculated by:

$$\text{Scale change factor} = \frac{12}{\text{focal length in inches}}$$

Most commercial aerial photos have the focal length in millimeters listed on the border (Example CFL208.36).

---

[2] *This program was originally written by Paul Ries, Routt National Forest, and is presented here with his permission.*

[3] *Derived from equations presented in Rayner and Schmidt (1963).*

User Instructions

1. Initialize program.
2. Select topographic map scale desired:
   Press **A** for 1:24,000 scale.
   Press **A′** for 1:62,500 scale.
3. Enter map distance, press **B**.
4. Enter photo distance, press **C**. Observe unadjusted scale.
5. Enter elevation of measurement, press **D**.
6. Enter the standard elevation desired for the photo (usually the average elevation of the photo's effective area), press **D′**. The scale computed in step 5 will be adjusted to the standard elevation and displayed.
7. Steps 3, 4, and 5 may be repeated as desired. The adjusted scale will now be displayed each time **D** is pressed.

To determine acreages:

1. Enter photo scale, press **B′**.
2. Enter photo scale elevation, press **R/S**.
3. Enter: Dot count (64 dots per square inch) of measured area, press **E** or planimeter reading (in square inches), press **E′**.
4. Enter mean elevation of measured area, press **R/S**. Scale and acres of measured area will print. Display will show acres.
5. Steps 3 and 4 can be repeated as needed.

Each measured area should be within the effective area of a photo. If the desired area falls within the effective area of two or more photos, the portion occurring in each should be measured separately.

Examples

Scale calculation:

Map distance = 1.75 inches
Photo distance = 2.5 inches
Elevation = 8,500 feet
Unadjusted scale = 16,800 @ 8,500 feet
Standard elevation = 9,000 feet
Adjusted scale = 16,070 @ 9,000 feet

Acreage determination:

Photo scale = 16,000 @ 9,000 feet
Dot count = 128
  or, planimeter reading = 2 square inches
Mean elevation of measured area = 9,200 feet
Scale of measured area = 1:15,708
Acreage = 78.67 acres

Program Outline

Key	Description
A	Initialize, 1:24,000 map scale CLEAR MEMORIES CLEAR FLAG 01 24,000 STORE 01 STOP
A′	Initialize 1:62,500 map scale CLEAR MEMORIES CLEAR FLAG 01 62,500 STORE 01 STOP
B	Enter map distance STORE 10 STOP
C	Enter photo distance and calculate unadjusted photo scale STORE 11 $\left(\frac{\text{RECALL 10}}{\text{RECALL 11}}\right)$ RECALL 01 = STORE 02 STOP
D	Enter elevation of measurement STORE 03 IF FLAG 01 is set: CALL SUBROUTINE 01 STOP
D′	Enter standard elevation STORE 04 SET FLAG 01 CALL SUBROUTINE 01 STOP
SUBROUTINE 01	Adjusts scale to standard elevation RECALL 04 - RECALL 03 = CHANGE SIGN x 1.46 = + RECALL 02 = STOP
B′	Enter photo scale and photo scale elevation STORE 05 STOP STORE 06 STOP

E	Enter dot count and elevation of measured area, calculate acreage ÷ 64 = CALL SUBROUTINE 02 STOP
E′	Enter photo area in square inches, calculate acreage CALL SUBROUTINE 02 STOP
SUBROUTINE 02	Calculates acreage and scale STORE 07 STOP (Enter elevation press RUN) – RECALL 06 = CHANGE SIGN x 1.46 = + RECALL 05 = X or scale of measured area on photo STOP (observe scale, press RUN) $\left(\frac{X^2}{6272640}\right)$ RECALL 07 = acrea STOP

Data Registers Used

01 = Map scale
02 = Unadjusted photo scale
03 = Elevation of map and photo distan measurements
04 = Standard elevation
05 = Adjusted photo scale
06 = Elevation of known photo scale used in acrea computation
07 = Measured photo area in square inches
10 = Map distance
11 = Photo distance

Spruce Variable Plot Cruising

This program brings the computational power of a large computerized inventory to the field, making possible instant reduction of cruise data and application of results. It is especially useful where no inventory information is available to write silvicultural prescriptions, to complete transportation system planning, or to perform presale layout.

With this program, the user can obtain quick summaries of board feet volumes and stocking from variable radius plot tally data. This program contains the general volume equations for Engelmann spruce, used in the multispecies board foot volume program, which was derived from data collected throughout the central Rockies (Myers and Edminster 1972). It can easily be modified for other species or other volume equations by changing subroutines 01 and 02 to include the desired equations.

To use this program, each "in" tree in a variable plot sample would be tallied on a sheet by 1 inch d.b.h. (midpoint 0.5 inch) and 10 feet total height class. The BAF used should result in several trees being tallied per point. The number of points sampled in the stand also should be noted.

Formulas Used

The midpoint of each d.b.h. class is used to compute basal area in square feet by:

$$BA = d.b.h.^2 \times 0.005454$$

For a single point, each tallied tree represents a ce tain number of trees per acre. This is found by dividin the BAF used by the BA of a given d.b.h. class.

$$\frac{BAF}{BA} = \text{No. of trees per acre for each tree tallied}$$

Dividing this figure by the number of plots taken result in an average trees per acre conversion factor for eac tree tallied in the stand.

Given the d.b.h. class, BAF, number of plots taken and the total number of trees tallied in that d.b.h. class the program uses the above equations to calculate th stems per acre for that d.b.h. class. A subroutine i then called to calculate the volume in board fee Scribner rule for a tree of the given d.b.h. and heigh class.

$$\text{Volume} = 0.01097\ D^2H - 15.14466 \text{ for } D^2H \text{ to } 12{,}200$$
$$\text{Volume} = 0.01202\ D^2H - 27.91343 \text{ for } D^2H > 12{,}200$$

This single tree volume is then multiplied by the stems per acre computed above to give a volume per acre for the d.b.h. class and height class. D.b.h. class volumes are accumulated to yield a total volume per acre for the stand. The program is designed to work through one d.b.h. class at a time. For example, all the 10-inch class data is entered and a summary is obtained before moving on to the 11-inch class. To minimize the chance for error, the program is designed to flash the display when all the required variables have not been entered.

Program Description

A Stores d.b.h. class midpoint.
B Stores height class. Computes D^2H.
C Stores the number of trees. Computes stems per acre. Assigns proper subroutine to compute volume.
D Displays d.b.h. volume per acre and stems per acre summary. Clears stem per acre and volume registers for another d.b.h. class.
E Displays total volume per acre and total stems per acre.
A′ Stores BAF.
B′ Stores the number of plots taken.
E′ Initializes the program by clearing all memories, clearing all flags, and resetting program pointer.

Internal Subroutines

Subroutine 01—supplies proper spruce regression functions to subroutine 02 according to D^2H.
Subroutine 02—calculates volumes for Engelmann spruce.

User Instructions

1. Initialize program.
2. Enter BAF, press **A′**.
3. Enter the number of plots, press **B′**.
4. Enter d.b.h., press **A**.
5. Enter height, press **B**.
6. Enter the number of trees tallied, press **C**.
7. Observe volume per acre for trees of the given d.b.h. and height. RECALL 15 will display the stems per acre.
8. Repeat steps 7-10 until all cells for a d.b.h. class have been loaded. BAF, number of plots, d.b.h. class, and height class can be entered in any order. All must be entered prior to entering the number of trees and pressing **C**.
   After entering the above data once, the only item which **must** be entered prior to pressing **C** again is the number of trees. The program will automatically use the BAF, number of points, d.b.h., and height data still stored in memory from the last computation to process the new number of trees entered. **The user need only enter data which has changed** from the last entry and not re-enter all data for each height or d.b.h. class. However, once a d.b.h. class total has been calculated by pressing **D**, a new d.b.h. class must be entered before continuing.
9. Press **D** for the total volume per acre for that d.b.h. class. Press RUN for stems per acre total for that class.
10. Go to step 4 and begin entering a new d.b.h. class.
11. Repeat steps above until all data has been entered.
12. Press **E** for the total volume per acre in the stand. To find total stems per acre, press RUN.
13. Go to step 1 to enter data from another stand.

Example

Figure 5 is an example of a cruise tally sheet and the volumes computed from it.

Program Outline

```
Key     Description

        INITIALIZE PROGRAM

A'      Store BAF
        STORE 11
        SET FLAG 03
        STOP

B'      Store number of points
        STORE 13
        SET FLAG 04
        STOP

A       Enter d.b.h. class, calculate
          midpoint
        d.b.h. + 0.5 =
        STORE 01
        SET FLAG 01
        STOP

B       Enter height class, calculate
          $D^2H$
        STORE 02
        $(\text{RECALL } 01)^2 \times \text{RECALL } 02 =$
        STORE 03
        SET FLAG 02
        STOP

C       Enter number of tally trees,
          calculate stems per acre and
          volume
        STORE 14
        IF FLAG 01 IS NOT SET:
          CALL SUBROUTINE 04 (This
            subroutine does not exist;
            therefore, an error results
            when it is called, aborting
            the program)
        IF FLAG 02 IS NOT SET:
          CALL SUBROUTINE 04
        IF FLAG 03 IS NOT SET:
          CALL SUBROUTINE 04
        IF FLAG 04 IS NOT SET:
          CALL SUBROUTINE 04
        $(\text{RECALL } 01)^2 \times 0.005454 = X$
        $\frac{1}{X}$ x RECALL 11 ÷ RECALL 13
          x RECALL 14 =
        STORE 15
        SUM 18
        SUM 09
        CALL SUBROUTINE 01
        STOP
```

Tally sheet

BAF 50 **No. points 5**

Height	50	60	70
d.b.h. 10	●		●
d.b.h. 11	● ● ●	●	●
d.b.h. 12		● ● ● ●	
d.b.h. 13			● ● ●

Stand volume table

Height	50	60	70	Totals	
d.b.h.				Volume	Stems per acre
10	753.8		1,156.1	1,909.9	33.3
11	2,387.2	996.8	1,198.0	4,582.0	69.3
12		4,116.4		4,116.4	46.9
13			3,785.7	3,785.7	30.2
			Total	14,394.0	179.7

Figure 5.—Example cruise tally sheet and stand volume table.

```
SUBROUTINE 01    Select regression functions for
                   volume calculations
                 IF RECALL 03 ≥ 12,200:
                   0.01202 STORE 04
                   27.91343 STORE 05
                 otherwise:
                   0.01097 STORE 04
                   15.14466 STORE 05
                 CALL SUBROUTINE 02
                 (VOLUME) x RECALL 15 =
                   (VOLUME/ACRE)
                 SUM 06
                 SUM 10
                 RETURN

SUBROUTINE 02    Calculate tree volume
                 RECALL 04 x RECALL 03 -
                   RECALL 05 = (VOLUME)
                 RETURN

D                Display d.b.h. totals, reset
                   memories for next d.b.h.
                   class
                 RECALL 10
                 STORE 07
                 RECALL 18
                 STORE 08
                 0.0 STORE 10
                 0.0 STORE 18
                 RECALL 07
                 STOP
                 RECALL 08
                 STOP

E                Display grand total volume and
                   stems per acre
                 RECALL 06
                 STOP
                 RECALL 09
                 STOP
```

Memory Registers Used

01 = d.b.h. class
02 = Height class
03 = D^2H
04 = First regression function
05 = Second regression function
06 = Stand volume total
07 = Temporary volume
08 = Temporary stems per acre
09 = Stand total stems per acre
10 = d.b.h. volume total
11 = BAF
12 = Not used
13 = Number of plots taken
14 = Number of tally trees
15 = Temporary stems per acre for a height class within d.b.h.
16 = Not used
17 = Not used
18 = d.b.h. stems per acre total

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Shepperd, Wayne D. 1980. Hand-held-calculator programs for the field forester. USDA Forest Service General Technical Report RM-76, 17 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

A library of programs written for hand-held, programmable calculators is described which eliminates many of the computations previously done by hand in the field. Programs for scaling aerial photos, variable plot cruising, basal area factor calibrations, and volume calculations are included.

Keywords: programmable calculator, photointerpretation, forest inventory, variable plot cruising

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U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

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Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Lubbock, Texas
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526

Status, Ecology, and Management of the Lesser Prairie Chicken

Maple A. Taylor and Fred S. Guthery

General Technical Report RM-77
Rocky Mountain Forest and
Range Experiment Station
Forest Service
U.S. Department of Agriculture

Abstract

This report assesses past and recent distribution of the lesser prairie chicken; summarizes knowledge of its life history, ecology, and management; and identifies research needs.

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Status, Ecology, and Management of the Lesser Prairie Chicken[1]

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and

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Department of Range and Wildlife Management
Texas Tech University

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Status, Ecology, and Management of the Lesser Prairie Chicken

Maple A. Taylor and Fred S. Guthery

MANAGEMENT IMPLICATIONS

The occupied range of lesser prairie chickens (*Tympanuchus pallidicinctus*) has decreased 92% since the 1800's, and the sandy prairies upon which these birds depend continue to be converted to cropland. Therefore, management should be directed at acquisition, preservation, and improvement of habitat.

Optimum habitat for lesser prairie chickens consists of mid to tall grass prairies for nesting and wintering cover interspersed with lower seral stages for feeding and brooding cover. Grazing systems that perpetuate higher successional grasses and leave adequate residual cover are essential for these birds. On those portions of lesser prairie chicken range that are infested with Havard oak (*Quercus havardii*), application of herbicides may improve habitat by increasing grass production.

Research is indicated to maintain or increase lesser prairie chicken populations and to improve their management. The response of these birds to weather, stocking rates, grazing systems, brush control, and various land management practices needs to be quantified so that sound advice can be given to land managers. Methods of censusing lesser prairie chickens need to be evaluated and improved. Lastly, successful transplanting techniques need to be developed because currently unoccupied habitat likely is available for re-introductions.

INTRODUCTION

The range of the lesser prairie chicken has shrunk dramatically since 1900, and in 1979 was restricted to isolated areas in New Mexico, Colorado, Kansas, Oklahoma, and Texas. Research on this species has been diverse, including basic life history, seasonal habitat requirements, food habits, and behavior. However, much more needs to be known about the ecology and habitat use of the lesser prairie chicken if its welfare is to be insured. To aid in orienting future research and management, we have synthesized available information on the status, ecology, and management of the lesser prairie chicken and have identified research needs.

TAXONOMY

Ridgway (1873) first described the lesser prairie chicken as a variety of the greater prairie chicken, designated *Cupidonia cupido* var. *pallidicincta*. He later (1885) re-evaluated the lesser prairie chicken to specific rank.

Short (1967) regarded the lesser prairie chicken as only racially distinct from *T. cupido*, a position supported by Johnsgard (1973). Based on detailed studies of morphology and behavior, Sharpe (1968) considered the lesser an allospecies. Conversely, Jones (1964a) supported specific distinction between the two based on differences in behavior, vocalization, morphology, and habitat use. Likewise, the American Ornithologists' Union (1957) recognizes the lesser prairie chicken as a distinct species.

DISTRIBUTION AND STATUS

Historical

Accurately determining the historical distribution of the lesser prairie chicken is difficult because early observers confused them with greater prairie chickens and, perhaps, because of their late recognition as a distinct species (Sharpe 1968). Nonetheless, early researchers agree that lesser prairie chickens inhabited the eastern portion of the Great Plains from southwestern Kansas and southeastern Colorado south through western Oklahoma and eastern New Mexico to west-central Texas. There may have been small populations in the sandy lands of northeastern Colorado and northwestern Nebraska. The area originally occupied by lesser prairie chickens, based on Aldrich's (1963, p. 537) map, was about 358,000 km^2.

Records summarized by Sharpe (1968) suggest that lesser prairie chickens migrated from breeding to wintering areas in the 1800's. Bent (1932) considered roughly the northern half of their original distribution as breeding range and the southern half as wintering range. Whether migrations to wintering areas were normal or only periodic responses to overpopulation, extreme food shortagres, or other phenomena is unknown.

It is difficult to envision gallinaceous birds making regular, long-distance migrations of the magnitude indicated by Bent (1932). Willow ptarmigan (*Lagopus lagopus*), rock ptarmigan (*L. mutus*), and blue grouse (*Dendragapus obscurus*)—the most mobile grouse—seldom migrate farther than 32 km (Weeden 1964, Zwickel et al. 1968). We suspect birds seen in the southernmost portions of their historical range were residents rather than migrants, because plant communities currently occupied by the birds were present in those areas.

Recent

By 1969, the range of the lesser prairie chicken had shrunk to 125,000 km², based on our measurement of Aldrich's (1963, p. 537) map, a 65% decrease from the 1800's. Although patchwork agriculture may have increased lesser prairie chicken numbers during 1900 to 1930 (Jackson and DeArment 1963), the species seems unable to tolerate areas with greater than 37% cultivation (Crawford and Bolen 1976a). Thus, widescale conversion of prairies to farmland has been primarily responsible for the decline in distribution and numbers of lesser prairie chickens.

Because the bird depends on medium and tall grasses preferred by cattle in regions of low rainfall, its habitat is easily overgrazed (Hamerstrom and Hamerstrom 1961). Overgrazing of rangeland was probably another cause of the population decline (Bent 1932, Lee 1950). The birds have disappeared from extensive blocks of Havard oak rangeland in some areas (e.g., Dickens County, Texas), where overgrazing is the most likely explanation for their demise. However, stable (but perhaps low) populations in heavily grazed Havard oak sandhills in west Texas indicate they can tolerate long-term grazing of high intensity.

Other factors implicated in the decline of lesser prairie chicken populations include overharvest during droughts of the 1930's and 1950's (when continental populations reached an all-time low) and extensive brush control (Jackson and DeArment 1963).

Colorado

By the late 1950's, the lesser prairie chicken was rare in Colorado and was found only in Kiowa, Prowers, and Baca counties (Hoffman 1963). The species is presently classified as threatened in this state (Torres et al. n.d.). There are two populations with a total of 400 to 500 birds.[2] One is small (2 gobbling grounds) and is southeast of Holly in Prowers County; the other is larger (20 gobbling grounds) and is near Campo in Baca County[3] (fig. 1). The latter population is primarily on the Comanche National Grassland, administered by the USDA Forest Service, although some birds can be found on private land south of the Cimarron River.[4] Lesser prairie chickens currently occupy about 1,634 km² in Colorado.

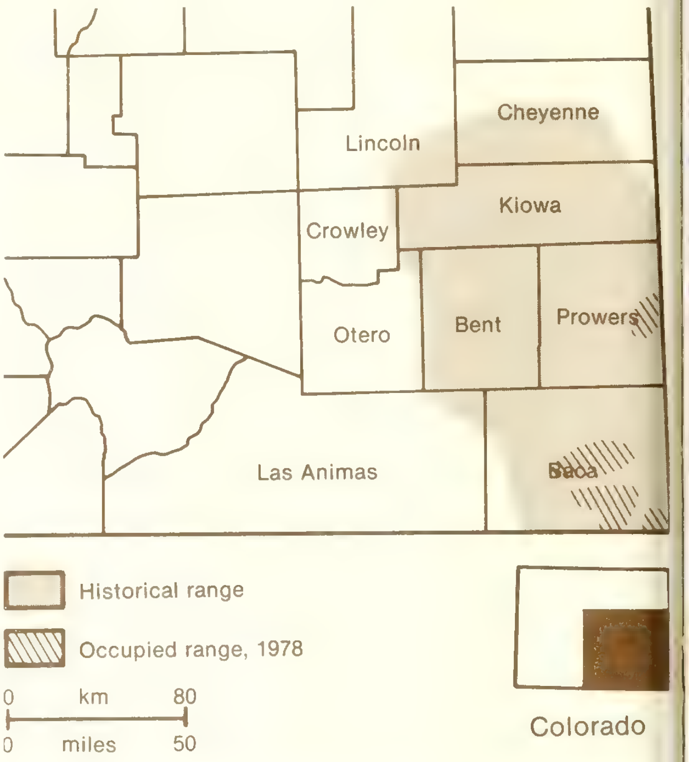

Figure 1.—Past and recent distribution of the lesser prairie chicken in Colorado.

Kansas

White[5] assessed the distribution of lesser prairie chickens in Kansas, finding only minor changes in occupied range since 1950. He reported the species was primarily restricted to areas near the Cimarron and Arkansas Rivers. The birds inhabited Hamilton, Stanton, and Morton counties eastward to Reno, Kingman, and Harper counties northward to Ness County (Waddell 1977). Gobbling grounds were found on 213 sections in 1976. Observations or reliable reports of sightings were noted for an additional 91 sections. Thus, occupied range included at least 778 km² (fig. 2), but most of Meade, Seward, Finney, Hamilton, Hodgeman, Clark, Comanche, Barber, Pratt, Stafford, and Kiowa counties needed further evaluation. Based on 1974 data and habitat conditions, there were about 17,000 lesser prairie chickens in Kansas (Waddell 1977).

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[2] *Personal communication, Ed Prenzlow, Division of Wildlife, Colorado Springs, Colo.*

[3] *Personal communication, Walter Graul, Division of Wildlife, Denver, Colo.*

[4] *Personal communication, Morris Snider, USDA Forest Service, Springfield, Colo.*

[5] *Unpublished manuscript, C. White, Kansas Forestry, Fish, and Game Commission, Pratt.*

klahoma

In Oklahoma, the range of the lesser prairie chicken hanged little from 1940 to 1957 (Copelin 1963). The irds were common in Beaver, Harper, Woodward, llis, and Roger Mills counties; occupied limited areas Beckham, Cimarron, and Texas counties; and were are in Blaine, Dewey, and Green counties. From 1957 to 1960 they extended their range in Wood, Dewey, and Harper counties. The current range of the lesser prairie chicken has many spatially separated populations and some isolated flocks (Cannon and Knopf 1978) (fig. 3). These data are tentative as distribution studies are still in progress,[6] but the birds occupy at least 1,355 km².

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[6] Personal communication, Fritz Knopf, Oklahoma State University, Stillwater.

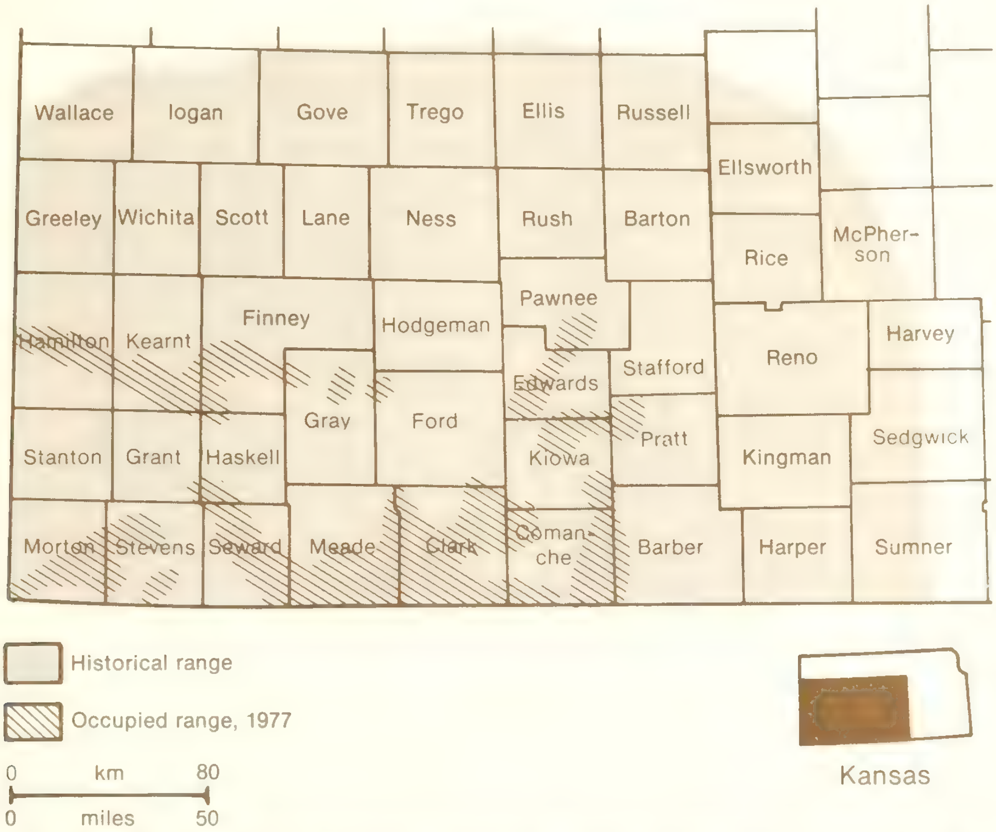

Figure 2.—Past and recent distribution of the lesser prairie chicken in Kansas (Waddell 1977).

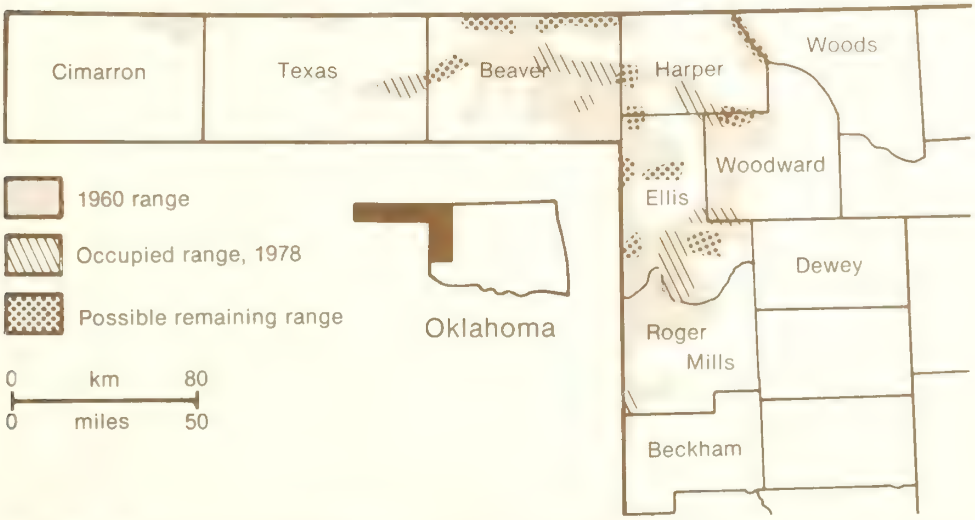

Figure 3.—Past and recent distribution of the lesser prairie chicken in Oklahoma (Cannon and Knopf 1978).

New Mexico

After the drought of the early 1950's, populations of lesser prairie chickens in New Mexico showed noticeable increases in 1956, peaked in 1959, and remained relatively stable through 1964 (Snyder 1967). During the peak, birds re-occupied much of their former range in southeastern New Mexico (fig. 4). Highest populations are found in Roosevelt and northern Lea counties. There are approximately 2,600 birds on U.S. Bureau of Land Management land in Chaves and Roosevelt counties.[7] Harvest data showed most birds were taken in Roosevelt, Lea, and Chaves counties, although there is also hunting in Eddy, Curry, and DeBaca counties (Sands 1978). Based on data presented by Campbell (1972), the average fall population of lesser prairie chickens in New Mexico is approximately 6,000-10,000 birds. Occupied range is about 18,898 km².

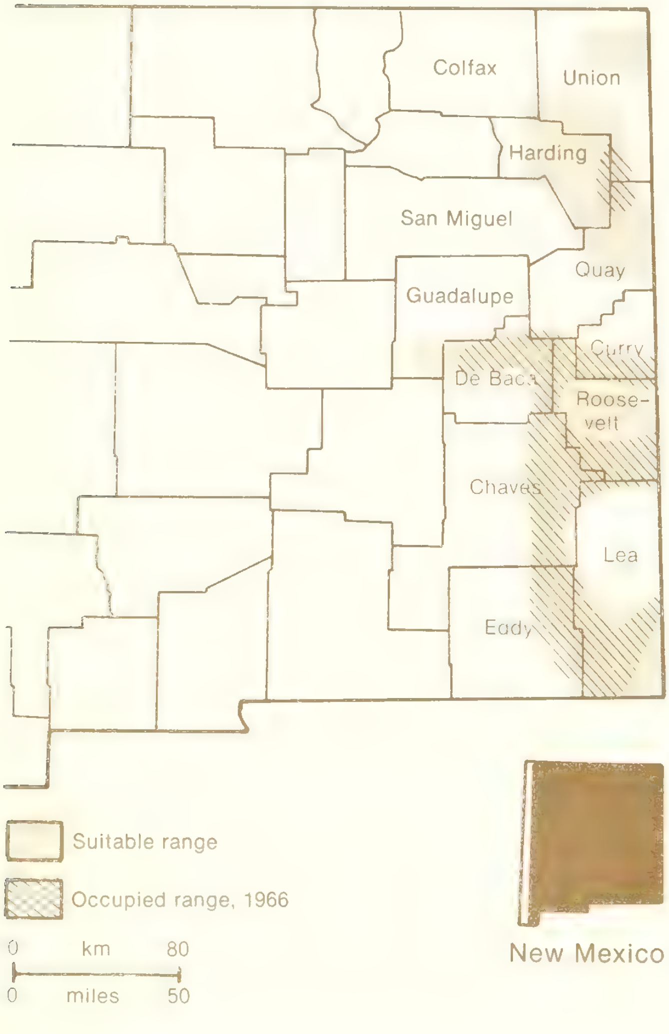

Figure 4.—Past and recent distribution of the lesser prairie chicken in New Mexico (Snyder 1967).

Texas

The range of lesser prairie chickens in Texas has decreased sharply since 1945 (fig. 5). Presently, two disjunct populations remain. The population in the northeastern portion of the panhandle occupies about 3,238 km² and sustains an annual harvest rate of 2%-3% (Litton 1978). The southwestern population occupies 1,388 km² and sustains an annual harvest rate of 10%-21%. Litton (1978) estimated the statewide population at 18,000 birds.

Overall

Lesser prairie chickens currently occupy a total of 27,300 km² in five states. This represents a 78% decrease in range since 1963 and a 92% decrease since the 1800's. To obtain a crude estimate of the current continental population, we multiplied lesser prairie chicken density in Texas (3.9/km²) by the minimum area occupied in Oklahoma (1,355 km²) to obtain a population estimate of 5,300 birds for the latter state. This figure was added to the range of values reported for other states to obtain an overall estimate of 46,700-55,330 birds.

Future

Conversion of sandy rangeland into farmland will continue to decrease the range and numbers of lesser prairie chickens. In Kansas, center-pivot sprinkler systems are permitting irrigation of lands formerly impractical, uneconomical, or technically impossible to farm (Waddell 1977). Sand prairies south of the Arkansas River, the heart of lesser prairie chicken range in Kansas, are disappearing at an average rate of 5% per year (Waddell and Hanzlick 1978). Habitat loss through conversion of rangeland to cropland in Finney, Grant, Gray, Haskell, and Kearney counties is expected to reduce the Kansas population to 9,500 birds (a loss of 7,500) by 1983 (Waddell 1977). In Colorado, center-pivot irrigation may soon eliminate the remnant prairie chicken population near Holly.[8] Texas has also seen development of center-pivot systems in the range of its lesser prairie chicken populations (fig. 5), but the extent of the development is unknown. Conversion of sandy rangeland to cropland may increase in Texas because water tables are relatively high in these areas and dropping in other portions of the High Plains.

Although conversion of sandy prairies into cropland will continue to decrease the range and numbers of lesser prairie chickens, some areas appear immune to such developments. Besides occupied range on state and federal land, some rangeland will not be converted because it cannot be farmed or because it is on large ranches whose owners are unlikely to begin farming. Limited areas of Havard oak rangeland in west Texas will not be cultivated because the City of Lubbock owns the water rights. Thus, it appears that enough habitat is available to maintain populations of lesser prairie

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[7] *Personal communication, Lynn Metz, Bureau of Land Management, Roswell, N. Mex.*

[8] *Personal communication, Ed Prenzlow, Division of Wildlife, Colorado Springs, Colo.*

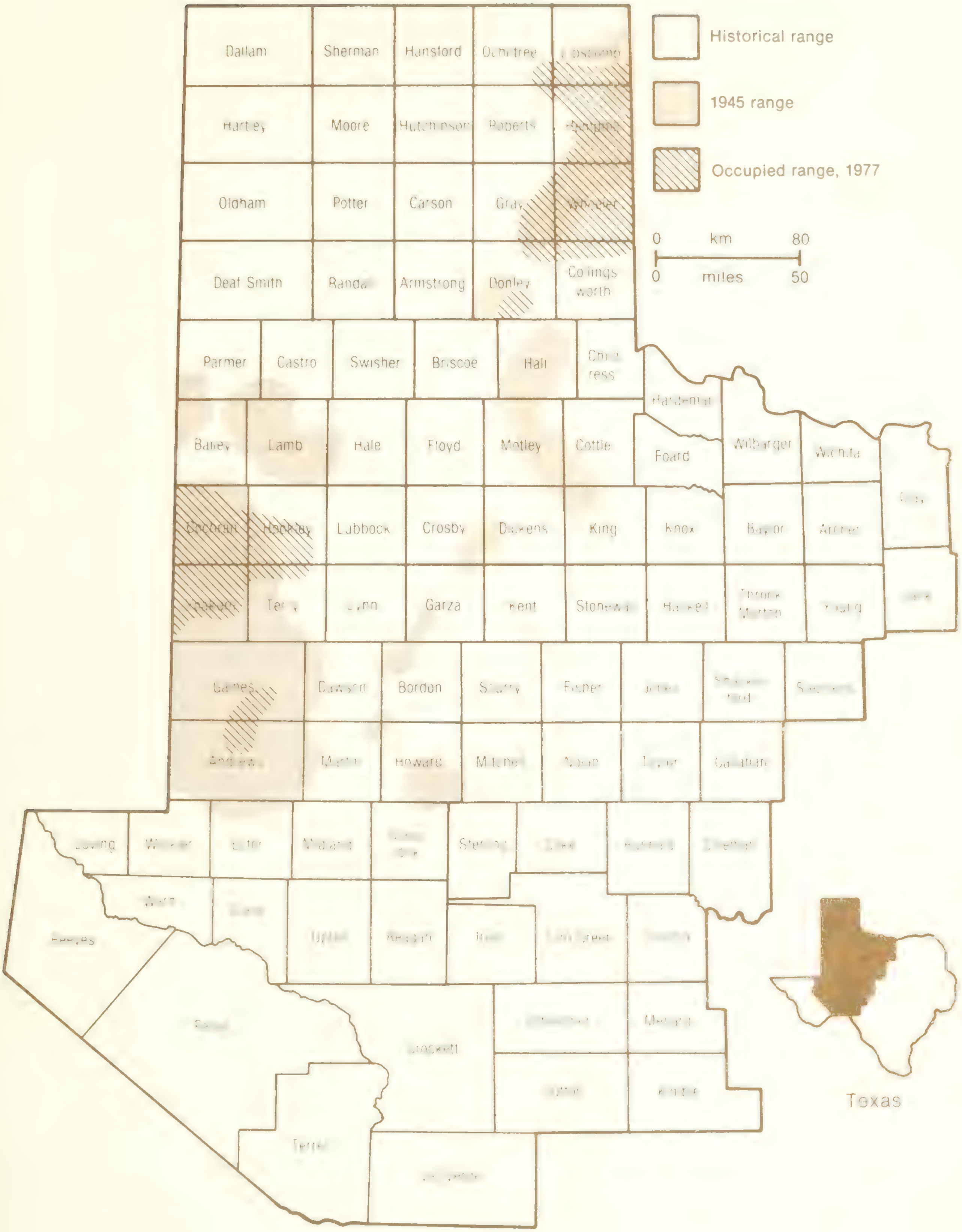

Figure 5.—Past and recent distribution of the lesser prairie chicken in Texas (Litton 1978).

chickens, perhaps indefinitely. Areas (km²) of public land occupied by lesser prairie chickens in 1979 are shown below:

State	Federal	State	Total
Kansas	142.6	33.8	176.4
Colorado	153.6	0	153.6
New Mexico	1,005.1	79.9	1,085.0
Oklahoma	0	37.6	37.6
Texas	0	20.0	20.0
	1,301.3	171.3	1,472.6

There are lesser prairie chickens on the Black Kettle National Grassland in Oklahoma, but this area consists of small tracts interspersed in private land.[9]

HABITAT

General Cover Requirements

Although the original habitat requirements of the lesser prairie chicken are poorly documented, these birds currently depend on mixed grass-dwarf shrub vegetation found on sandier soils (Jones 1963a). Two general habitat types, sometimes interspersed with shortgrass prairie on loamy to clayey soils, are suitable: (1) sand sagebrush (*Artemisia filifolia*)-bluestem (*Andropogon* spp.), and (2) Havard oak-bluestem (Jones 1963b). The sand sagebrush type is predominantly in Colorado, Kansas, and Oklahoma, with some areas in New Mexico and Texas; the Havard oak type is in Oklahoma, Texas, and New Mexico. The distribution of these vegetation types (Kuchler 1964) conforms well with the distribution of lesser prairie chickens in the 1800's (Sharpe 1968).

The sand sagebrush-grassland community occupied by lesser prairie chickens in Colorado is dominated by sand sagebrush, little bluestem (*A. scorparium*), switchgrass (*Panicum virgatum*), sideoats grama (*Bouteloua curtipendula*), and red threeawn (*Aristida longiseta*).[10]

In Kansas, the highest densities of lesser prairie chickens are south of the Arkansas River in sand sagebrush prairies similar to those in southeastern Colorado (Sexson and Horak 1978). A few flocks remain, however, on sand prairies dominated by mid to short grasses.

Copelin (1963) found lesser prairie chickens in western Oklahoma using three vegetation types. The Havard oak type was composed of mid and tall grasses (sand bluestem (*A. hallii*), little bluestem, sand dropseed (*Sporobolus cryptandrus*), and sideoats grama), a variety of forbs, and Havard oak. The sand sagebrush type had mixed grasses, especially buffalograss (*Buchloe dactyloides*), hairy grama (*B. hirsuta*), and blue grama (*B. gracilis*), and dense sand sagebrush. The mixed-grass prairie type was composed of tall, mid, and short grasses, some forbs, and sand sagebrush. Copelin (1963) found that birds used areas of 80%-100% rangeland more than areas with 10%-80% rangeland.

Although there are lesser prairie chickens in a variety of habitat types in New Mexico, they are most abundant in Havard oak and sand sagebrush rangelands (Frary 1956). The Havard oak type dominates southern portions of lesser prairie chicken range in New Mexico; sand sagebrush prevails to the north. Mid and tall grasses, including sand bluestem, big bluestem (*A. gerardi*), little bluestem, yellow Indiangrass (*Sorghastrum nutans*), prairie sandreed (*Calamovilfa longifolia*), and grama grasses, probably dominated the climax vegetation of these areas, with lesser amounts of yucca (*Yucca* spp.), Havard oak, sand sagebrush, mesquite (*Prosopis* spp.), and fragrant sumac (*Rhus aromatica*).

In Texas, the lesser prairie chicken inhabits sand sagebrush and Havard oak grasslands north of the Canadian River and Havard oak to the south and west (Jackson and DeArment 1963). The sagebrush-grassland type is characterized by sand sagebrush, sand chickasaw plum (*Prunus angustifolia watsoni*), and fragrant sumac. Havard oak dominates in the Havard oak association; sand sagebrush and fragrant sumac occur in lesser amounts. The two types have the same grasses: sand bluestem, little bluestem, sand dropseed, and switchgrass. Crawford and Bolen (1976a), working in the Havard oak sandhills of west Texas, considered 23-km² areas with 63%-95% native rangeland and the balance in grain farming better habitat than areas with 100% native rangeland. Areas with less than 63% rangeland appeared incapable of sustaining populations. Crawford and Bolen (1976a) also found that density of lesser prairie chickens was positively correlated with the proportion of an area occupied by deep sand range sites.

Seasonal Variation in Habitat Use

Lesser prairie chickens are associated with various components of their overall habitat depending on phenological changes in the availability of foods and coverts (Jones 1963a) and seasonal weather. Researchers in Oklahoma have analyzed seasonal changes in habitat use with life-form criteria. The single-most important vegetation life form, by covert function and season, as determined for lesser prairie chickens in Oklahoma, is shown below. (Short or dwarf is less than 25 cm tall; mid is 25 to 80 cm tall; tall is more than 80 cm tall. A shrub is a stem branched from the base, more than 80 cm tall; a half-shrub has lower parts lignified, upper parts herbaceous; a tree has a distinct main trunk remaining unbranched in lower parts. Short life forms surrounded by taller life forms were used throughout the year.)

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[9] *Personal communication, Bill McCaslan, Oklahoma Department of Wildlife Conservation, Shattuck.*

[10] *Personal communication, Walter Graul, Division of Wildlife, Denver, Colo.*

Function and season	Author	
	Jones (1964a)	Donaldson (1969)
Feeding		
Winter	Tall grass	Short grass
Spring	Dwarf half-shrub	—
Summer	Mid forbs	Short grass
Fall	Mid grass	Short grass
Resting		
Winter	Dwarf half-shrub	Mid grass
Spring	Dwarf half-shrub	Short grass
Summer	Dwarf half-shrub	Dwarf shrub
Fall	Dwarf half-shrub	Mid grass
Roosting		
Winter	Short life forms	Mid grass
Spring	Short life forms	—
Summer	Short life forms	Mid grass, dwarf shrub
Fall	Short life forms	Mid grass
Escape		
Winter	—	Mid grass
Spring	—	—
Summer	—	Tree
Fall	—	—

The differences reported by these authors probably reflect the fact that Jones (1963) was working in a sand sagebrush prairie, whereas Donaldson (1969) combined data from treated (sprayed) and untreated sand sagebrush and Havard oak associations. The data are oversimplified because lesser prairie chickens are associated with several life forms for various activities during all seasons, particularly spring. These birds require a diversity of life forms within their home range.

On a plant community basis in New Mexico, Davis et al. (1979) found that Havard oak-sand bluestem areas with the highest percentage of sand bluestem generally were preferred throughout the year over areas with decreasing percentages of sand bluestem and increasing percentages of Havard oak. However, fall-winter feeding sites were in areas with more Havard oak, probably because of the availability of acorns. Mesquite-shortgrass communities were least preferred throughout the year.

Taylor (1978) and Sell (1979) studied habitat use of lesser prairie chickens on a heavily overgrazed site in the Havard oak sandhills of west Texas. During summer, females were found most often in areas with the highest Havard oak coverage and height and areas with the greatest diversity of forbs and grasses. Although the birds apparently foraged in sandhills with high densities of Havard oak during morning and evening in fall and winter, they preferred Havard oak-sand sagebrush flats and shinnery oak-bluestem communities. Birds avoided mesquite-Havard oak, mesquite-blue grama, and reverted cropland communities or used them incidentally to foraging in a sunflower field.

Taller trees and shrubs, if available, are used for shade during the summer when temperatures approach or exceed 23.6° C (Copelin 1963). Plants used include Havard oak, sand sagebrush, fragrant sumac, and sand chickasaw plum.

Many investigators have documented the use by and importance of crops to lesser prairie chickens during fall and winter. Jones (1964b) found that the birds ate sorghum when available, unless fragrant sumac was amply present. In west Texas, sorghum is an important component of the diet (Crawford and Bolen 1976b), as are sunflowers if available (Taylor and Guthery 1980b).

Foods

The diet of young lesser prairie chickens is 85% (Jones 1963a) to 99% (Davis et al. 1979) insects, mostly grasshoppers (Orthoptera) and beetles (Coleoptera). Broods spend considerable time foraging in plant communities with high percentages of forbs because there are more insects in these areas (Jones 1963a).

Studies conducted in the sand sagebrush grasslands in Oklahoma (Jones 1963a) and the Havard oak-tall grass community in New Mexico (Davis et al. 1979) suggest general similarities in the diet of adult lesser prairie chickens and differences representing adaption to available food supplies. For example, mast and seeds constituted the lowest percentage of the diet in both areas during spring, and animal matter (almost exclusively insects) was over 50% of the summer diet (fig. 6). Data from both studies reveal that dicotyledons contribute the vast majority of plant foods to the lesser prairie chicken diet.

However, foliage constituted about 80% of the spring diet in New Mexico, consisting largely of Havard oak catkins, annual eriogonum (*Eriogonum annuum*) leaves, and broom snakeweed (*Gutierrezia sarothrae*) leaves (Davis et al. 1979). Foliage, mainly of big-headed evax (*Evax prolifera*) and sixweeks fescue (*Festuca octoflora*), constituted only about 50% of the spring diet in Oklahoma (Jones 1963a). Insects were more important in Oklahoma than in New Mexico, although this finding may be an artifact of the two methodologies. Jones analyzed droppings, which yield an upward bias in the proportion of hard foods, such as insect fragments, passing intact through the digestive tract, whereas Davis et al. (1979) analyzed crop contents.

During fall and winter, mast from Havard oak was 39.2% and 69.3%, respectively, of the diet of birds in New Mexico (Davis et al. 1979). However, in Oklahoma, insects were the principal dietary item during fall (Jones 1963a). Foliage, principally leaf and flower buds of fragrant sumac, leaves of sand sagebrush, and leaves of broom snakeweed during snow cover, and annuals such as sixweeks fescue, annual eriogonum, Ivarian violet (*Viola kitaibeliana*), and big-headed evax (when available) were about 70% of the winter diet.

Crawford and Bolen (1976b) found that plant and animal matter comprised 81% and 19%, respectively, of the volume of foods in the fall diet of lesser prairie chickens in west Texas. Grain sorghum, Havard oak (leaves, acorns, and galls), and short-horned grasshoppers together were 70% of the volume.

Water

Lesser prairie chickens drink free water (from stock ponds) during spring (Crawford and Bolen 1973, Sell 1979), summer and fall (Copelin 1963, Jones 1963a, Sell 1979), and early winter (Taylor 1978). That the birds inhabited arid regions prior to development of water supplies indicates they do not require abundant free water (Snyder 1967, Crawford and Bolen 1973).

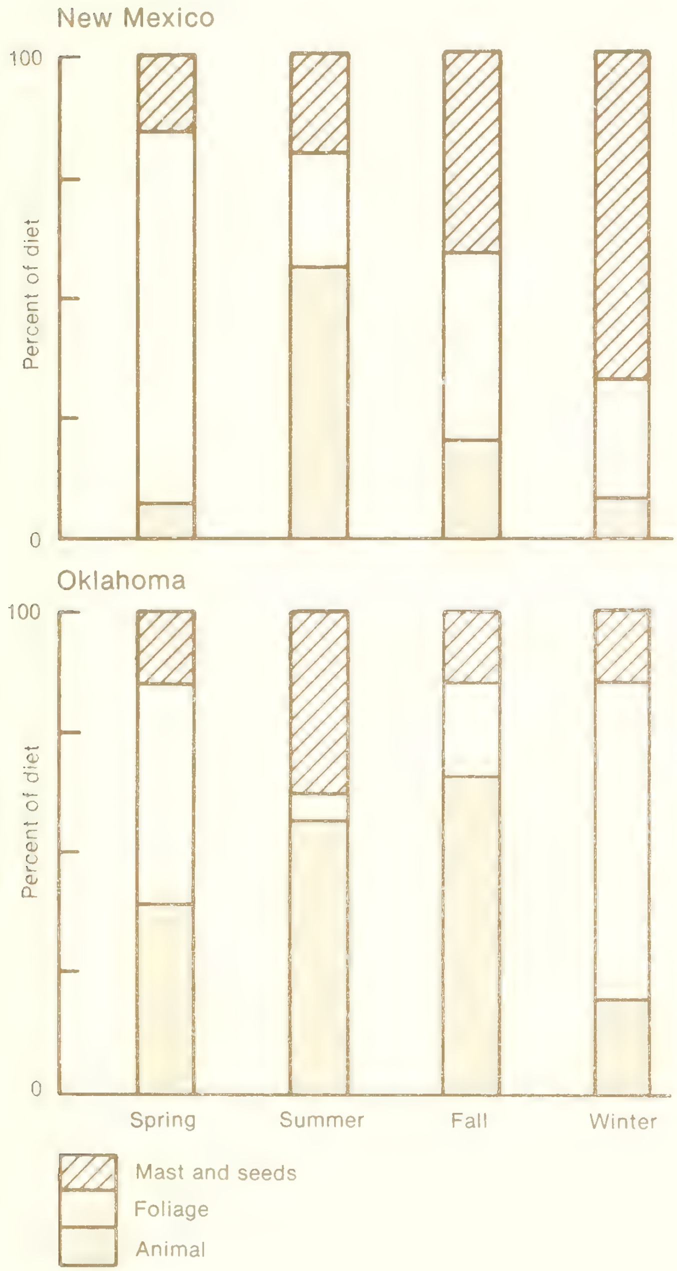

Figure 6.—Relative volumetric proportions of mast and seeds, foliage, and animal matter in the diets of lesser prairie chickens from New Mexico (Davis et al. 1979) and Oklahoma (Jones 1963a).

LIFE HISTORY

Lekking

Lesser prairie chickens congregate on leks (also termed display grounds, arenas, gobbling grounds, and—somewhat erroneously—booming grounds) for courtship displays in spring and fall. Leks are relatively void of vegetation and are usually on ridges where visibility is good (and perhaps where calls can be heard for greater distances). Copelin (1963) found that most leks are in short grass areas on slightly elevated terrain, but some are on flats. In the sand sagebrush vegetation type, display grounds are in valleys on shortgrass meadows if sand sagebrush is tall and dense. Jones (1963a) found leks on ridges where mean height of vegetation was 10.39 cm. Donaldson (1969) found most leks on ridges, but some were in large swales. He found that if the vegetation on leks grows rapidly, the leks are abandoned earlier in the season than leks where growth is slower. Cannon and Knopf (1979) observed leks on small ridges among scattered clumps of little bluestem.

In west Texas, undisturbed leks in native rangelands average more males than do leks subject to human disturbance (Crawford and Bolen 1976c). They found leks on oil well pads, roads, reverted cropland, and cultivated land. Taylor (1980) located 14 leks, separated by an average of 1.2 km to the nearest lek, on a 5,200-ha block of Havard oak rangeland. Two natural leks were on slightly elevated terrain where Havard oak was 10-20 cm tall. The remaining 12 leks were on open areas created by man, including oil well pads, tilled fields, and experimental plots treated with tebuthiuron.

Jones (1964a) found lesser prairie chickens on courtship grounds throughout the year except August and December. During early spring, when chasing is the primary activity, few birds establish regular territories, fighting is irresolute and lasts less than 1 minute, and birds are restless and easily flushed by raptors (often not returning to the lek until the next day). (We have flushed birds during spring trapping up to three times in the same morning with birds returning each time.) Calls are weaker than in late spring, when copulation takes place. As spring progresses, territories become more firmly established, defense of territories increases, and some birds fight continuously during morning. In late spring and early summer, little gobbling or fighting is seen, and the birds spend much time resting and preening.

Donaldson (1969) and Crawford (1974) found the most males on leks in late April and early May. Hens are present from March to May, but most are seen in April, when counts of males are more uniform (Donaldson 1969). The number of males using leks both early and late in the season varies considerably; usually more birds are on leks in mornings than evenings. Activity decreases during late May to mid June.

Fall lek activity begins early in September (possibly late August). Fighting and gobbling usually are of low intensity at this time (Copelin 1963, Jones 1963a, Donaldson 1969), but occasionally approach the intensity of spring display (Donaldson 1969). In September, young males join adult males on leks, and in October hens appear (Copelin 1963). There are fewer birds on grounds by November, and activity decreases. During fall, territories are smaller, closer together, and more poorly defined than they are in spring (Jones 1964a, Taylor 1978). Birds usually do not return to leks when flushed, suggesting a less intensive drive to display. Daily visits to display grounds cease in late October or November, possibly because of foul weather (Copelin 1963) and, in some areas, to grain crop feeding.

Sharpe (1968) described lesser prairie chicken calls, courtship, and display in much greater detail than presented here. Grange (1940), Hjorth (1970), Robel (1970), Ballard and Robel (1974), and Wiley (1974, 1978) also present related information.

Lesser prairie chicken cocks show high fidelity to leks where they have established territories (Campbell 1972). Of 17 banded males identified two or more seasons, 15 occupied the same territory on leks and two changed locations but remained on the same ground (Copelin 1963). Of 55 leks mapped in 1930, Copelin found 28 in use in 1960, demonstrating the permanency of traditional sites. Many leks, however, were not used in one or more intervening years.

Females and juvenile males probably show less tendency to remain associated with a single lek than do adult males. Greater prairie chicken hens may visit several leks before mating, and if the nests are destroyed, may go to a different lek for remating. Cocks, mostly juveniles, visit different grounds when attempting to establish territories (Robel et al. 1970). We have seen interlek movements by banded juvenile lesser prairie chickens and the relocation of one banded adult male following break up of a lek overgrown with dense vegetation.

Certain factors cause a lek to be abandoned. Use may cease if vegetation becomes too tall or dense (Schwartz 1945, Hamerstrom et al. 1957), presumably interfering with the need to see and be seen during courtship displays. Lesser prairie chickens in Oklahoma have relocated leks to freshly burned sites nearby (Cannon and Knopf 1979).

Nesting and Brooding

Lesser prairie chicken hens frequent leks, where copulation occurs, from mid-March through mid-May (Copelin 1963). Nesting activities peak near mid-May (Snyder 1967).

Hens lay 11-14 grayish-olive or buffy-plain or spotted eggs (41.9 by 32 mm) (Bent 1932) in about 14 days (Snyder 1967) and incubate them about 23 days (Trippensee 1948). Hens renest when the first nest is lost early in incubation or before incubation begins; second nests are seldom begun if the loss is late in incubation (Edminster 1954). The precocial young leave the nest within hours.

Bailey (1928) described the nest as "a slight excavation in the open or among grass or weeds, sparingly or thickly lined, according to abundance of material at hand, with grasses and a few feathers." Copelin (1963) similarly found nests-bowls scratched in the sand, about 10.2 cm deep and 20.3 cm across, lined 3.8 cm deep with Havard oak leaves and grasses. Sell (1979) described nest bowl depth and diameter as 7.2 and 19.0 cm, respectively. Donaldson (1969) noted nests "scooped out" in sand 5 cm deep and 18 cm across, approachable through a west-facing tunnel. Riley (1978) found nests within small depressions, 15 m or less from small hills (1-2 m tall) located to the south, southwest, or west of the nest site. This orientation may have protected hens from high winds.

Bent (1932) found two nests under sand sagebrush in Kansas. Copelin (1958) found three nests situated between clumps of little bluestem, dropseed, and threeawn from the previous year's growth. Later, he found seven nests located between grass clumps, two under sand sagebrush, and one under Russianthistle (*Salsola kali*). No nests were found among shrubs more than 35 cm high. Jones (1963a) found a nest in a half-shrub short grass community consisting of purple threeawn (*A. purpurea*) and sand sagebrush, comprising 55% and 17%, respectively, of total plant cover. Vegetation averaged 45 cm high at nests. Donaldson (1969) found a nest in little bluestem, Scribner's panicum (*P. oligosanthes*), and Havard oak. Vegetation height at the nest ranged from 32-52 cm.

Sell (1979) studied nesting in the Havard oak sandhills of west Texas and found six of eight nests where the topography was relatively flat; Havard oak was lower and less dense and forb and grass frequencies were higher than in the surrounding community. Sand sagebrush overhung five of eight nests, two were in clumps of purple threeawn, and one was in dense Havard oak. He found an increase ($p<0.01$) in sand sagebrush canopy and structural density at nest sites.

Riley (1978) studied the nesting ecology of the lesser prairie chicken in Havard oak-tall grass and mesquite vegetation types in southeastern New Mexico. Of 18 nests, 16 were found in habitats with high canopy coverage by tall, perennial grasses. There was progressively more sand bluestem and total grasses within 90, 9, and 3 m of the nests. Havard oak, total shrubs, and total forbs decreased correspondingly. The average height of plants within 9 m of nests (28.5 cm) was less than ($p<0.10$) the average height of cover directly above nests (60.6 cm). There was a higher percentage of grasses within 3 and 9 m of nests in which young were hatched than near nests in which no young were hatched. Nests were hidden by dry vegetation from the previous year. Some data suggested that dense shrubs may substitute for grasses in providing security for nests.

Comparisons between the data of Sell (1979) and Riley (1978) indicate when tall grasses are less abundant, the lesser prairie chicken becomes more dependent on brush species (particularly sand sagebrush) for nesting. Sell's study area was heavily overgrazed (unlike Riley's), and most nests were concealed by sand sagebrush.

Lesser prairie chicken broods use portions of available habitat that are in lower seral stages. In Oklahoma, areas for brooding are shrub and half-shrub sites with more forbs than are found in areas used for other activities (Jones 1963b). In west Texas, brood use was highest on areas with the most active sand dunes and the greatest coverage and height of Havard oak (Sell 1979). Broods in New Mexico preferred habitats with a lower percentage of sand bluestem and a higher percentage of Havard oak; the average height of vegetation in foraging sites was 25.3 ± 14.6 cm (Riley 1978). Copelin (1963) found 27 broods in Havard oak motts and one in low Havard, which apparently reflected their need for shade during the summer.

When broods are 8-10 weeks old, the hen leaves them and molts. The broods associate and form early fall flocks; by mid-September they begin visiting leks.

Population Characteristics

Sex Ratios

The presence of slightly more males than females may be normal for lesser prairie chicken populations. Davison (1940) found male:female ratios of 1:0.71, 1:0.68, and 1:0.61 in broods. The sex ratio of hunter-killed birds during 6 years in New Mexico ranged from 1:0.53 to 1:1.25; the ratio for the total sample (1,718 birds) was 1:0.77 (Snyder 1967). Campbell (1972) reported the ratio of 2,447 birds to be 1:0.73. Lee (1950), however, found a 1:1 ratio in 923 birds. The overall ratio for the samples of adult birds reported above is 1:0.78 (56% males, 44% females). It is unknown whether or not males and females are differentially susceptible to harvest. Therefore, the sex ratios reported above for adults may be biased, because they are based on bag checks.

Age Ratios

Juveniles usually outnumber adults in the hunting bag. The adult:juvenile ratio in New Mexico during 6 years ranged between 1:0.60 and 1:2.19 and was 1:1.01 for the sample of 1,718 birds (Snyder 1967). Campbell (1972) and Lee (1950) reported ratios of 1:1.20 and 1:1.14 for 2,447 and 923 birds, respectively. The overall age ratio for the above sample is 1:1.12 (47% adults, 53% juveniles). Again, it is unknown whether or not adults and juveniles are differentially susceptible to harvest; so, it is unknown whether or not the above age ratios represent the population.

Mortality Rates

Campbell (1972) has published the only data on the mortality rates of lesser prairie chickens. His analysis of 285 banded males indicated an annual mortality rate of 65%, which presumably was inflated 5% to 10% by failure to recapture banded birds. The period required for complete population turnover was calculated as 5 years.

The average percentage of juveniles in the fall population approximates the annual mortality rate if the population is stable. Thus, the percentage of juveniles (53) reported earlier for combined age ratio data roughly represents annual mortality. This figure is consistent with Campbell's (1972) analysis when the bias discussed above is taken into consideration.

Densities

Density estimates of lesser prairie chickens invariably have been derived from early morning counts of lekking males and must, therefore, be negatively biased because females are excluded. In Oklahoma, reported densities of males were 16.6-27.9 (Davison 1940), 13.5-16.2 (Jones 1963a), and 1.5-18.3 per section (259 ha) (Copelin 1963). If the combined male:female ratio (1:0.78) reported earlier is unbiased, the above densities can be multiplied by 1.78 to account for females in the population.

Movements and Home Ranges

The yearly home range of lesser prairie chickens during the 1800's apparently was larger than in modern times because of migration. It is impossible to determine the lengths of former migration, but Leopold (1933) considered the yearly cruising radius of prairie chickens to exceed 160 km. Migration of lesser prairie chickens is unknown in modern times, but residents of New Mexico have reported flocks traveling 40 km to grain fields (Frary 1956).

Daily mobility varies by sex, age, and season. Sell (1979) reported average minimum daily movements of 0.16-0.56 km for hens in west Texas during spring and summer. Daily movements gradually decreased from April through September, and the average minimum home range was 41.4 ha. Taylor and Guthery (1980b), working on the same areas as Sell (1979), reported October through February daily movements of 0.39-0.70 km for adult males, 0.50-1.07 km for juvenile males, 0.39-0.69 km for adult females, and 0.27-1.23 km for a single juvenile female. Minimum home ranges during fall and winter were 50-365 ha for adult males, 331-1,945 ha for juvenile males, 62-202 ha for adult females, and 35-495 ha for the juvenile female. During December, a juvenile male moved 12.8 km from the lek where trapped in 5 days or less, coincident with a passing cold front (Taylor and Guthery 1980a). Daily movements and home ranges increased from November through December and decreased from January through February.

Lesser prairie chickens apparently confine most of their activities within a radius of 3-4 km from the leks they use. In west Texas, eight hens captured on leks moved an average distance of 1.2 km to nest sites (Sell 1979). Taylor and Guthery (1980b) reported over 50% of locations of telemetered birds to be within 1.6 km of the lek where the birds were captured, 90% within 3.2 km, and 97% within 4.8 km. Only during December and January did a juvenile male range further than 4.8 km from the lek. Copelin (1963), similarly, reported 79% of relocations within 3.2 km of the point of capture, 93% within 4.8 km, and 97% within 6.4 km. In New Mexico, the mean distance moved between the lek where a bird was banded and point where it was recovered was 8.8 km for juveniles and 3.4 km for adults (Campbell 1972).

Data on movements and ranges allow inferences on the minimum area required by a lesser prairie chicken population. The lek is the focal point of yearly activity because display grounds are relatively permanent and because territorial males return to the same lek each year. It appears that an area with a radius of 3.2 km centered about a lek ($32\ km^2$) would meet minimum requirements of a lek population because about 90% of yearly activity occurs inside this limit (Taylor and Guthery 1980b). Circular areas of $72\ km^2$ would contain all activity except for some juvenile movements.

RESEARCH AND MANAGEMENT TECHNIQUES

Sex Determination

Because the plumage of male and female lesser prairie chickens is superficially similar, distinguishing sex of birds is difficult in the field. However, only cocks gobble and strut (females occasionally display weakly). Hence, females can be identified by their relative passivity on leks.

Sex is easily determined if specimens can be examined. Adult males have a supra-ocular comb that is lacking in females and poorly developed in juvenile males; males have black undertail coverts with a white "eye" near the tip of the tail whereas females have brown-barred undertail coverts (Ammann 1944); males have blackish tailfeathers with only the central feathers mottled or barred, whereas females have extensively barred tailfeathers (Copelin 1963); and the neck pinnae of males are 53-74 mm long, whereas the neck pinnae of females are rudimentary (because of molt, this character is not valid in fall) (Bailey 1928, Copelin 1963, Johnsgard 1973). Adult and juvenile cocks usually weigh more than hens (table 1).

Age Determination

Several plumage characteristics allow differentiation between young-of-year and adult lesser prairie chickens (Copelin 1963). The two outer primaries of juveniles have worn and frayed trailing edges whereas the outer primaries of adults lack such wear; the fore edge of the outermost primary of juveniles is spotted to the tip whereas that of adults is spotted only to within 2-3 cm of the tip; the shaft of the outer primary covert is light distally in juveniles whereas it is dark throughout in adults.

Enumeration

The number of males on leks and the number of leks in area may reflect population size (Hoffman 1963), although this has never been documented, and spring counts of gobbling cocks are used to determine trends in lesser prairie chickens populations. Because lekking activity is most intense during April and early May (Donaldson 1969, Crawford 1974), this appears to be the best time to make counts. Counts conducted from dawn to about 2 hours after daylight apparently show exceptional consistency, while afternoon counts are more variable (Davison 1940, Crawford and Bolen 1975). Overcast, rainy, or windy weather may stifle courtship behavior, so counts should be conducted on calm, clear days. In west Texas, we found substantial variation in fall counts of males on leks, suggesting

Table 1.—Mean weights (g) of lesser prairie chickens[1]

	Males				Females			
	Adult		Juvenile		Adult		Juvenile	
Source	n	weights	n	weights	n	weights	n	weights
Frary 1959	1	759	15	715	11	671	12	658
Taylor[2]	9	806	17	736	1	660	9	671
Taylor 1978	9	854	5	812	2	705	2	645
Sell 1979	11	750	10	748	10	740	9	706
Grand mean		789		740		702		674

[1] *Reported mean weights (sample size in parentheses) where sex and age were not determined are 715 g (700) (Lee 1950) and 781 g (5) (Baker 1953) and where age was not determined are 784 g (20) and 763 g (8) for males and 732 g (5) and 749 g (4) for females (Lehman 1941 and Frary 1957, respectively).*

[2] *Unpublished data.*

counts in this season would give imprecise indexes of population size.

Counts of males on gobbling grounds can be used to estimate population size if the proportion of females in the population is known. Moreover, it must be assumed that all males in the population display, or the proportion of nondisplaying males must be known.

Capture

Several techniques have been successfully used to capture lesser prairie chickens. Ligon (1946) used lead traps along feeding routes and Schwilling (1955) modified Ligon's trap for use at water. Copelin (1963) used the Davison[11] drive net when birds were in the shade of Havard oak motts. Mist nets have been used successfully at water troughs during dry springs (Davis et al. 1979) and on leks. In the latter case, three or four nets were arranged in a semicircle on one side of the lek and birds were flushed into them (Campbell 1972). Also, mist nets were successful when positioned on leks between the territories of displaying males in spring (Taylor 1978). Etheridge (1943) caught 104 birds in 3 days using a baited drop net during winter when food was scarce, and Sell (1979) caught hens at water with a drop net. Cannon and rocket nets have been used to capture prairie chickens on leks (Ammann 1957, Taylor 1978).

The relative efficiency of techniques used to capture lesser prairie chickens is largely undocumented. Riley (1978) found hens, which were more difficult to catch than cocks, less wary of cannon nets than of mist nets. Our experience indicates mist nets positioned between territories are considerably less effective than rocket nets when capturing birds on leks during the fall because fighting and chasing are less intense than in spring and the birds generally are more wary. However, Silvy and Robel (1968) had better success capturing greater prairie chickens with mist nets than with cannon nets because of fewer recaptures, greater selectivity for hens, less disturbance, and lower costs. Drop nets probably are the best technique if used over bait or water during nonlekking periods.

Habitat Management

General Principles

The goal of habitat management for lesser prairie chickens should be to maintain sandy rangeland in good to excellent condition with a diversity of plant life forms and with "good" interspersion of taller woody cover and lower successional areas. Achieving this goal is largely a function of grazing management and, in portions of lesser prairie chicken range, selective control of Havard oak.

Any grazing system which promotes or maintains midsuccessional to climax grasses and which leaves adequate residual cover would benefit lesser prairie chickens. Thus, rotation, deferment, or moderate use of pastures is required.

Havard oak is exceedingly dense on some rangelands occupied by lesser prairie chickens, and the birds may increase with reduction of this plant (Donaldson 1969, Crawford 1974). Once established, the oak competes successfully with herbaceous vegetation and must be controlled to improve growth of grasses and forbs and improve habitat.

Fire and mechanical methods control Havard oak temporarily, but subsequent resprouting forms denser stands than before treatment (McIlvain 1956). Burning may increase production of sand bluestem and switchgrass while decreasing the production of little bluestem. During the year of burning, Havard oak acorns will be eliminated (McIlvain and Armstrong 1966). Frary (1955) believed fire of little benefit to lesser prairie chickens and warned of severe wind erosion following burning.

Foliar and root-absorbed herbicides, when applied properly, may be effective in controlling Havard oak and promoting growth of herbaceous vegetation (McIlvain 1954, Deering 1972, Pettit 1979). By varying the herbicide and its application rate, it is possible to mediate the response of Havard oak, grasses, and forbs.

Control of Havard oak must be done in a way that increases the diversity of habitat types. Control of extensive blocks could be counterproductive. Strip or topographical patterns (control flats and leave Havard oak on sandhills or other areas subject to erosion) offer the greatest potential for improving lesser prairie chicken habitat. Key habitat features, such as Havard oak motts, should be left intact.

Special Techniques

Although several habitat management techniques have been proposed, none has been evaluated. Nonetheless, the following recommendations are based on known ecological requirements of lesser prairie chickens.

Foot plots.—Planting grain sorghum within 1.6 km of leks may provide winter food when natural foods are scarce (Jones 1963a, Donaldson 1969, Crawford 1974). However, supplemental feeders and food plots were not used by birds in New Mexico (Snyder 1967). Copelin (1963) found only 1 of 35 food plots used when natural foods were abundant, but all were used when natural foods were scarce. Supplemental foods may be essential following extensive herbicidal treatment of Havard oak because acorn production will be low for about 2 years (McIlvain 1956). The attractiveness of cropland to lesser prairie chickens can be enhanced by minimum tillage (Crawford 1974).

[11] *Unpublished manuscript, Verne E. Davison, Oklahoma Department of Game and Fish, Oklahoma City.*

Grazing exclosures.—Grazing exclosures have been proposed to increase residual cover and thereby improve nesting and wintering habitat. Exclosures maintained on the Comanche National Grassland in Colorado averaged 6% more ground cover than grazed areas and resulted in improved nesting cover.[12] Davis et al. (1979) tentatively recommended 64-ha exclosures. Grazing exclosures are an expensive means of habitat improvement, and care must be taken not to create scattered islands of habitat where predation can become serious.

Water development.—Stock tanks may enhance survival of lesser prairie chickens during droughts (Crawford and Bolen 1973).

Lek development.—Clearing traditional display grounds overgrown with vegetation may enhance their value to the birds (Jones 1963a, Donaldson 1969, Taylor 1980). New space for lekking may be beneficial in extensive areas of dense vegetation (Jones 1963a, Crawford and Bolen 1976c, Taylor 1980). Sites should be slightly elevated with short, scattered vegetation (10-20 cm tall), within 3.2 km of suitable nesting and wintering habitat (Taylor 1980), and free of disturbances by man (Crawford and Bolen 1976c). Grounds should be at least 1.2 km away from active leks or use may be minimal (Taylor 1980).

RESEARCH NEEDS

There is much yet to learn about the ecology and management of lesser prairie chickens. Some of our present knowledge is tentative because of small samples and limited geographic or temporal scope. Thus, almost any facet of lesser prairie chicken ecology is worthy of further study. However, the topics enumerated below seem most essential for maintaining, multiplying, or managing the current resource.

Using multiple regression analysis, Crawford and Bolen (1976c) identified percentages of an area in rangeland, minimum tillage agriculture, and deep sand range sites as key habitat features for lesser prairie chickens in west Texas. This type of study needs expansion to include effects due to weather, stocking rates, grazing systems, and brush control practices. Because about 95% of currently occupied lesser prairie chicken range is on private land, it is essential we understand the effects of land use and management on the species. Armed with this knowledge, we can soundly advise individuals or agencies wishing either to increase populations of lesser prairie chickens or to minimize harmful effects of land management.

The above study presumes a high level of accuracy in enumeration of lesser prairie chickens if results are to be valid. However, there is no guarantee that the traditional spring counts of displaying males accurately reflect population size. First, such counts exclude females and, therefore, year-to-year variation in sex ratios renders the counts suspect. Second, we do not know the proportion of males in the population that displays, nor do we know the effects of lek size and density on this proportion. Additional detailed studies of daily and seasonal chronology of lek use would also help refine enumeration techniques.

Probably some areas formerly occupied by lesser prairie chickens provide suitable but unused habitat today. These areas need to be identified and successful transplanting techniques developed and implemented. Specifically, we need to know how many birds of what age and sex to release and what season is best for release. Attempts to re-establish lesser prairie chickens in Texas have failed for unknown reasons.[13]

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This report assesses past and recent distribution of the lesser prairie chicken; summarizes knowledge of its life history, ecology, and management; and identifies research needs.

Keywords: *Tympanuchus pallidicinctus*

Agriculture—CSU, Fort Collins

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

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*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526

USDA
Forest Service

Rocky Mountain Forest & Range Experiment Station
General Technical Report RM no. 78 is a map and
can be found in the back of this issue in the
envelope.

Arizona Range Reference Areas

Raymond M. Turner, Lee H. Applegate,
Patricia M. Bergthold, Steve Gallizioli,
and S. Clark Martin

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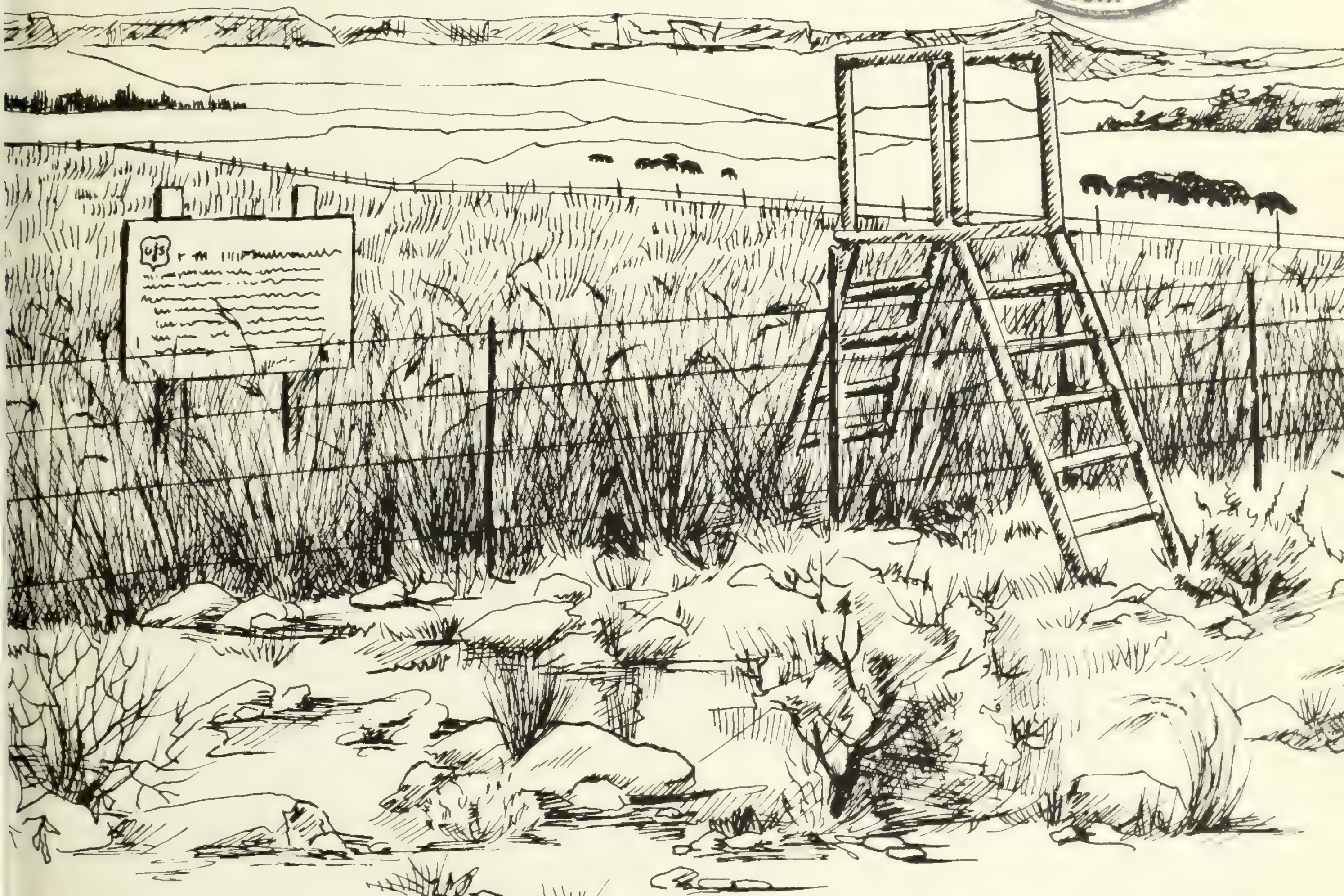

General Technical Report RM-79
Rocky Mountain Forest and
Range Experiment Station
Forest Service
U.S. Department of Agriculture

Turner, Raymond M., Lee H. Applegate, Patricia M. Bergthold, Steve Gallizioli, and S. Clark Martin. 1980. Arizona range reference areas. USDA Forest Service General Technical Report RM-79, 34 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Range reference areas (exclosures and remote areas) provide a historical record of vegetation that has not been influenced by livestock grazing. In Arizona, 380 exclosures can be used for research and management. Location, controlling agency, year of establishment, and vegetation information are provided for each reference area.

Keywords: Natural areas, range exclosures, range management, Arizona.

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Plant a tree! Mark the 75th birthday of the Forest Service by giving a living gift to future generations.

USDA Forest Service
General Technical Report RM-79

November 1980

Arizona Range Reference Areas

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Arizona Range Reference Areas

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INTRODUCTION

Most Arizona rangeland probably has been grazed by livestock for more than a century. Changes in vegetation on some of these rangelands are so marked and so extensive that current concepts of natural vegetation are based on landscapes that are quite unlike those present before human obtrusion. Much of this vegetation change has been attributed either directly or indirectly to livestock grazing. The role of grazing in changed southwestern landscapes can be evaluated by comparing vegetation of grazed and ungrazed tracts on similar sites. Opportunities for such comparisons in Arizona are limited to a few "remote" areas that have not been accessible to livestock because of distance from water or by rugged topography and to areas where livestock have been excluded by fencing.

In the early 1900's, several areas on western rangelands were fenced to permanently exclude livestock. These "exclosures," established by various agencies, were used to evaluate grazing impacts and to serve as standards for judging range condition. Other exclosures were designed to test interactions between livestock and big game or livestock and rodents. Another class of range reference area includes lands that have not been grazed by livestock because of physiographic inaccessibility. Because these tracts have always been protected from domesticated herbivores, they are especially useful in judging human influence on similar, adjacent tracts.

References from which to judge vegetation changes are essential for many ecological studies of rangeland resources. Range reference areas may provide isolated, relatively stable enclaves in surrounding natural ecosystems that are changing rapidly, or even vanishing, as land-use patterns change. As human impact on the environment increases, the value of reference areas will increase (Moir 1972).

For these reasons, the Society for Range Management (SRM) established the Reference Area Program in 1966 (Anderson 1966, Laycock 1975). The objective of this program has been to publish a comprehensive list of exclosures and remote areas on rangelands in North America. To date, compilations for Wyoming (Williams 1963), Utah (Laycock 1969), and Nebraska (Nebraska Section 1973) have been published.

In 1973, a team that included representatives from two state and two federal agencies began compiling this list for Arizona. The Arizona State Parks Board, as administrator of the State's Natural Areas Program, has interest in rangeland reference areas; the Arizona Game and Fish Department uses exclosures and remote areas as part of its wildlife research program; the USDA Forest Service similarly uses exclosures and remote areas for wildlife habitat and range research as well as for judging range conditions and trends on its grazing lands; and the U.S. Geological Survey has an interest in such areas for studies of the relationships between vegetation change and climate change, and between soil erosion and vegetative cover.

Those who use this list of reference areas should be aware of its limitations. Some of the exclosures are so small that perimeter effects influence their value. The records used as a source of data for this compilation are not complete, and, in most cases, the person administratively responsible for the reference area has no first-hand knowledge of when or under what conditions it was established. Consequently, those wishing use of a reference area may need to do some further checking. Although most of the published entries were checked by the agencies, any errors remain the responsibility of the authors. Readers are asked to report any exclosures or remote areas omitted.

EXAMPLE EXCLOSURES

Measurements, notes, and photographs from reference areas provide a partial account of changes that have occurred. Four examples are included.

In northern Arizona, much former grassland has been occupied by juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus edulis*) and small shrubs (snakeweed [*Gutierrezia microcephala*] and rabbit brush [*Chrysothamnus nauseousus*]). Biological Survey Plot No. 2 (Area 275) was built on the Kaibab National Forest in 1918 to study interactions between prairie dogs (*Cynomys gunnisoni*) and cattle. At that time, Taylor and Loftfield (1924) stated that the edge of the pinyon-juniper formation was a short distance from the plot, that the overgrazing had progressed so far that the grasses were more than half replaced by shrubs such as snakeweed and rabbitbrush and that washing was quite noticeable as evidenced by exposed grass roots. A photograph of the plot by W. P. Taylor, August 11, 1929, shows former grassland dominated by small shrubs with pinyon-juniper woodland in the background (fig. 1a). Many small trees can be seen in and around the woodland, a clear sign that the woodland was expanding by this early date. By 1978, juniper and other shrubs occupied the plot and obscured much of the background that was visible in 1929 (fig. 1b). This pair of photographs illustrates an important limitation that must be remembered when interpreting exclosures. Most, if not all, were established after at least several decades of grazing. Even after long-term livestock exclusion, conditions of the pregrazing era may not quickly return, especially if erosion and plant conversions have progressed far.

Changes in the Sonoran Desert landscape have been less striking perhaps than those in northern Arizona. Near Tucson, the Carnegie Institution of Washington fenced an 869-acre tract in 1907 for its Desert Botanical Laboratory at Tumamoc Hill (Area 109). The area had probably been grazed frequently by livestock for at least 20 years and may have been grazed sporadically much longer. Shreve (1937) stated that grazing probably was not great enough to seriously disturb the larger plants but that numbers of grasses and smaller perennials probably were greatly reduced. Records of vegetation observed on a plot 10 meters square in 1906 (fig. 2a) and 1978 (fig. 2b) show that the number of woody and succulent plants increased from 53 in 1906 to 269 in 1978. Plant densities in 1906 and 1978 are compared below for the four species with greatest abundance during each of those years:

	1906	1978
Yellow paper-flower (*Psilostrophe cooperi*)	32	0
White-thorn acacia (*Acacia constricta*)	6	4
Fendler hedgehog cactus (*Echinocereus fendleri*)	4	1
Jumping cholla (*Opuntia fulgida*)	2	0
Triangle-leaf bursage (*Ambrosia deltoidea*)	0	242
Creosotebush (*Larrea tridentata*)	1	7
Christmas cactus (*Opuntia leptocaulis*)	0	5

Perhaps it is noteworthy that none of the woody or succulent plants present is considered to be a valuable forage plant. The most striking changes are the loss, by 1978, of yellow paper-flower and the appearance of large numbers of triangle-leaf bursage. Because both plants are unpalatable to livestock, this species change cannot be attributed directly to cessation of grazing and is assumed to be the result of differences in the ways individual species respond to each other and to drought, freezing, or other climate factors.

Much semidesert rangeland in southern Arizona that was grassland in 1900 is now dominated by velvet mesquite (*Prosopis velutina*). Examples of this change have been photographed on the Santa Rita Experimental Range. The Range was fenced and all cattle were removed in 1903. Grazing resumed as grazing studies were expanded about 1912, and a number of exclosures were established within the grazed area between 1916 and 1920. The site of one of these exclosures (Area 189) was photographed first in 1905 (fig. 3a) and fenced in 1918. Grass stands that were cut for hay in 1905 became much too sparse for such use and were overtopped by moderate stands of mesquite in 1961 (fig. 3b).

Another Santa Rita exclosure (Area 200) was built in 1921 and is near permanent water in an area that is grazed all year. Mesquites reportedly were only 12-13 inches tall in 1923. Photographs taken along the fence line in 1930, 1952, and 1978 show progressive development of the mesquite stand inside the exclosure as well as outside (figs. 4a, 4b, and 4c). The two earliest photographs show the grass on the outside to be closely cropped in contrast to the taller ungrazed stand inside. By 1978, however, a second change had occurred. The dominant native perennial grasses, sprucetop grama (*Bouteloua chondrosioides*) and slender grama (*B. filiformis*), had been largely replaced by Lehmann lovegrass (*Eragrostis lehmanniana*). The new grass, an introduced species, is less palatable than the native perennial grasses, and it grows more vigorously in the presence of mesquite. The lack of apparent difference in grass cover caused by cattle exclusion in 1978, therefore, probably resulted from the cattle grazing native perennial grasses in other parts of the pasture instead of grazing Lehmann lovegrass around the exclosure.

DESCRIPTION OF INCLUDED INFORMATION

An inventory form was used to obtain information from agencies responsible for exclosures and remote areas. The form used (fig. 5) was a modificiation of that devised by Laycock (1969). These forms were distributed to several agencies during the spring of 1977.

The information published in this report is presented in the following order:

Agency.—This item gives the name of the owner or agency with administrative responsibility for the land on which the reference area is located. Names of USDA Forest Service or Bureau of Land Management districts appear as subheadings.

If other than the land owner or managing agency has built or maintained the exclosure, the cooperating agency is noted by abbreviation in parentheses after the name of the exclosure:

PL	Private land
AGF	Arizona Game and Fish Department
SCS	Soil Conservation Service
BLM	Bureau of Land Management
UA	University of Arizona
ARS	Science and Education Administration (formerly Agricultural Research Service)

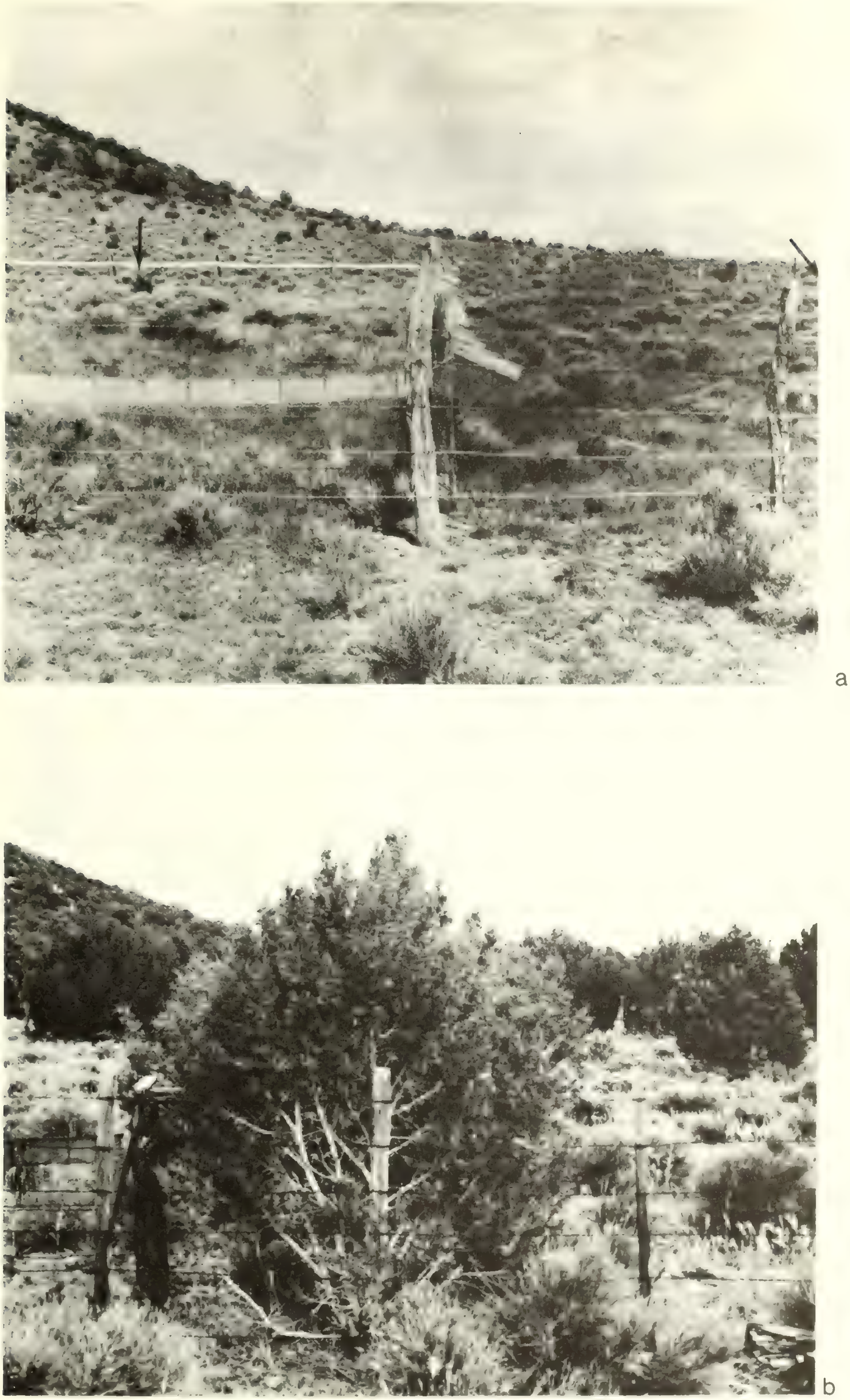


Figure 1.—Vegetation change in northern Arizona. (a) Plot fenced in 1918 (area 275) supported a mixture of small shrubs and grasses with pinyon and juniper in background in 1929. Arrow marks a small juniper. (b) By 1978, juniper grew densely in the plot. The conspicuous grass is bottle-brush squirrel tail (*Sitanion hystrix*). Other grasses present are blue grama (*Bouteloua gracilis*) and sand dropseed (*Sporobolus cryptandrus*).

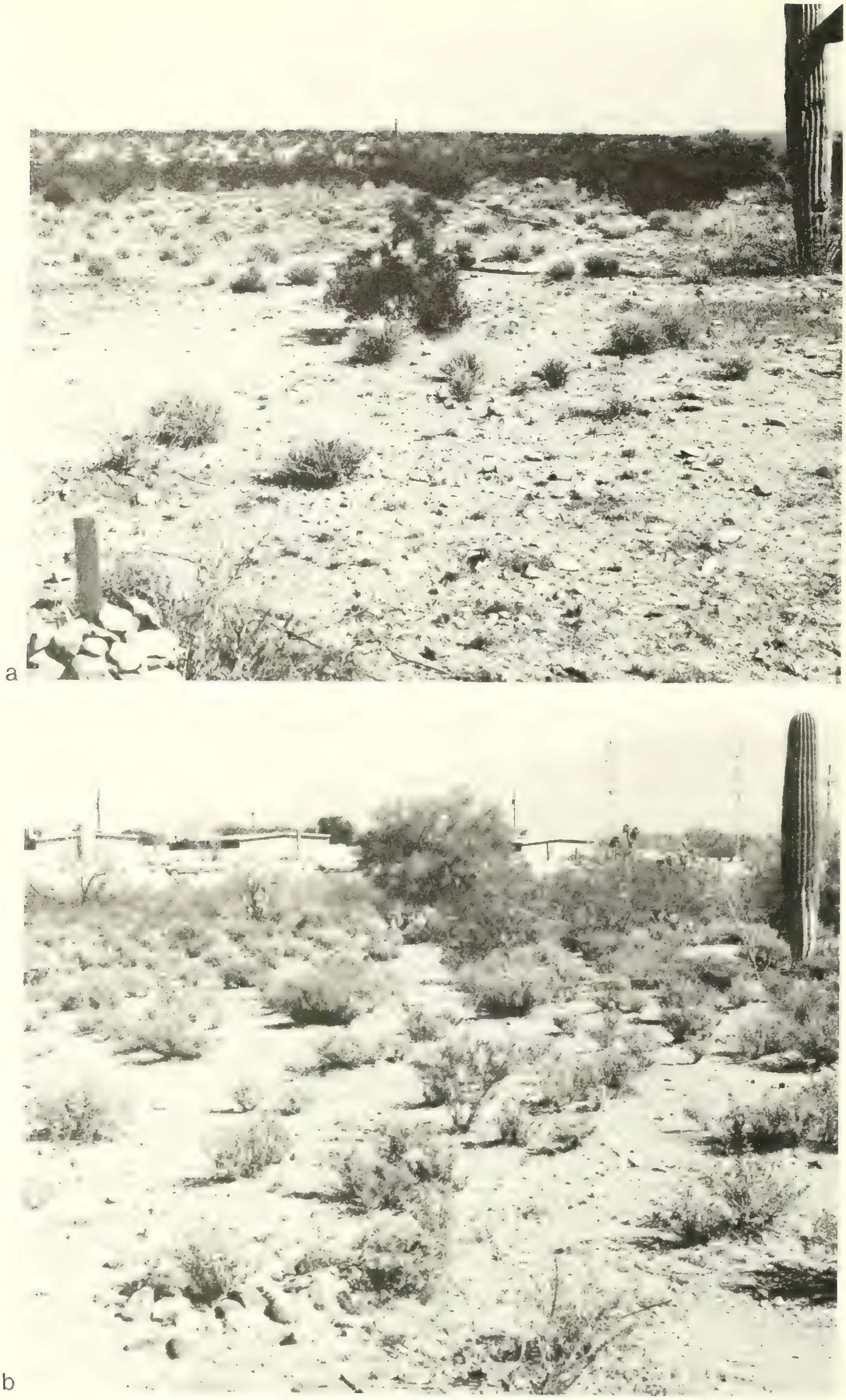


Figure 2.—Seventy years of desert vegetation change near Tucson, Ariz. (area 109). (a) Condition of vegetation shortly before livestock were excluded (picture was taken in 1906)—the dominant low shrub was yellow paper-flower (*Psilostrophye cooperi*). (b) Seventy-two years later (1978)—the dominant low shrub now is triangle-leaf bursage (*Ambrosia deltoidea*).

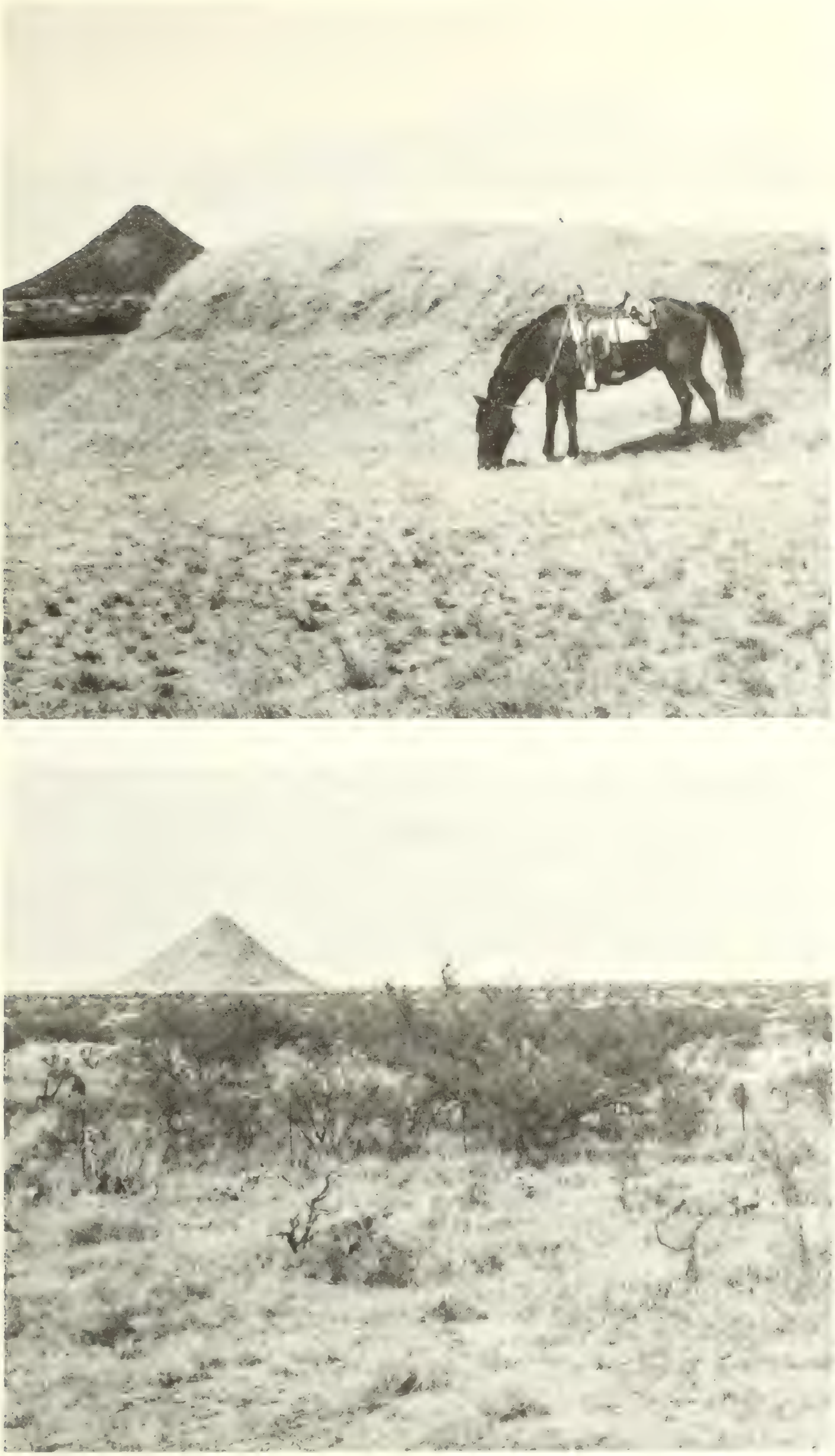


Figure 3.—An example of change from grassland to shrubland. (a) A pile of native grass hay cut from the Santa Rita Experimental Range two years after cattle were fenced out (1905). (b) The same area 56 years later (1961) supports a moderate stand of velvet mesquite and sparse perennial grass cover. Mesquite has become established in the exclosure (Area 189), built in 1918, at about the same rate as on grazed range.

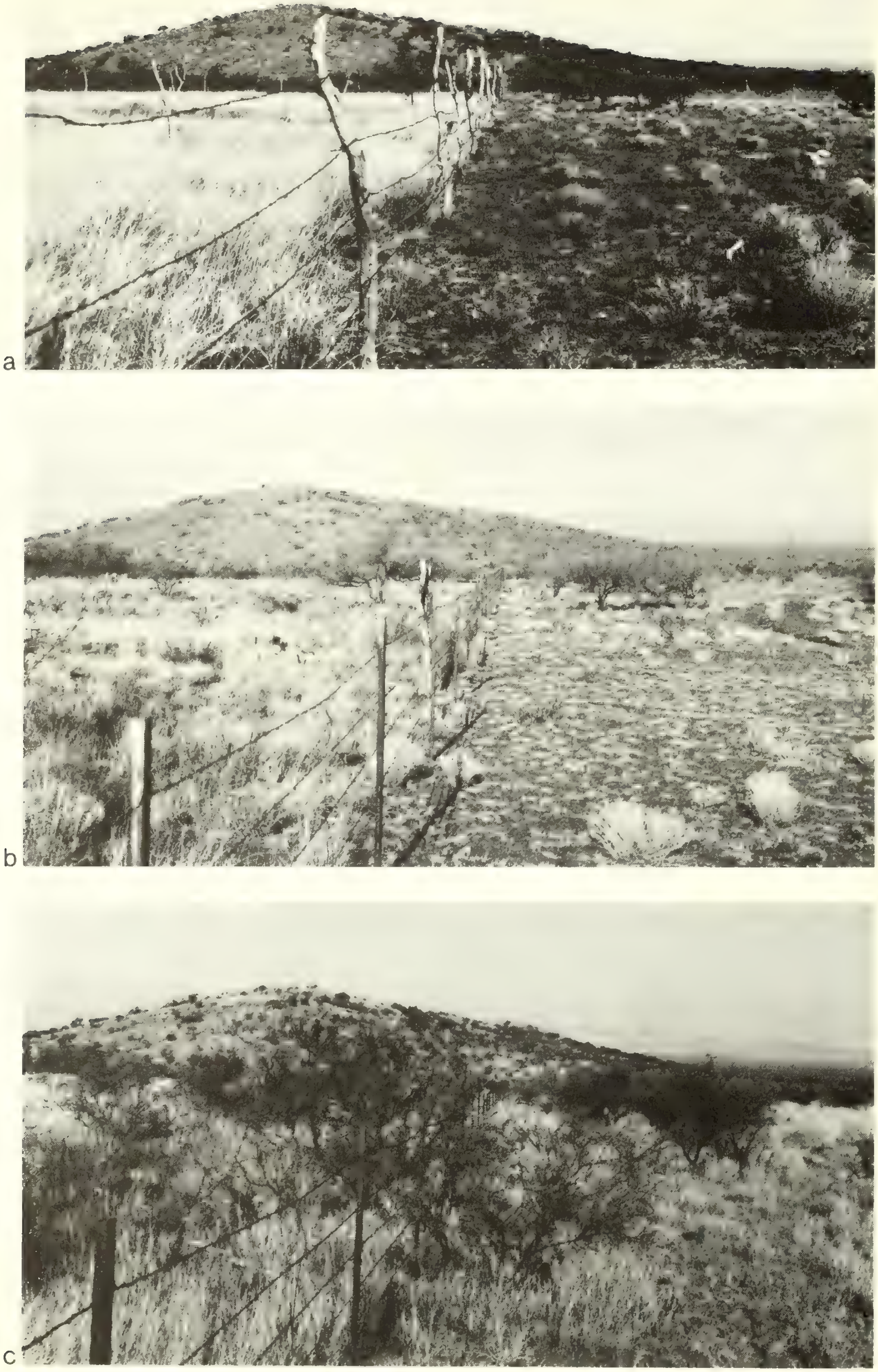
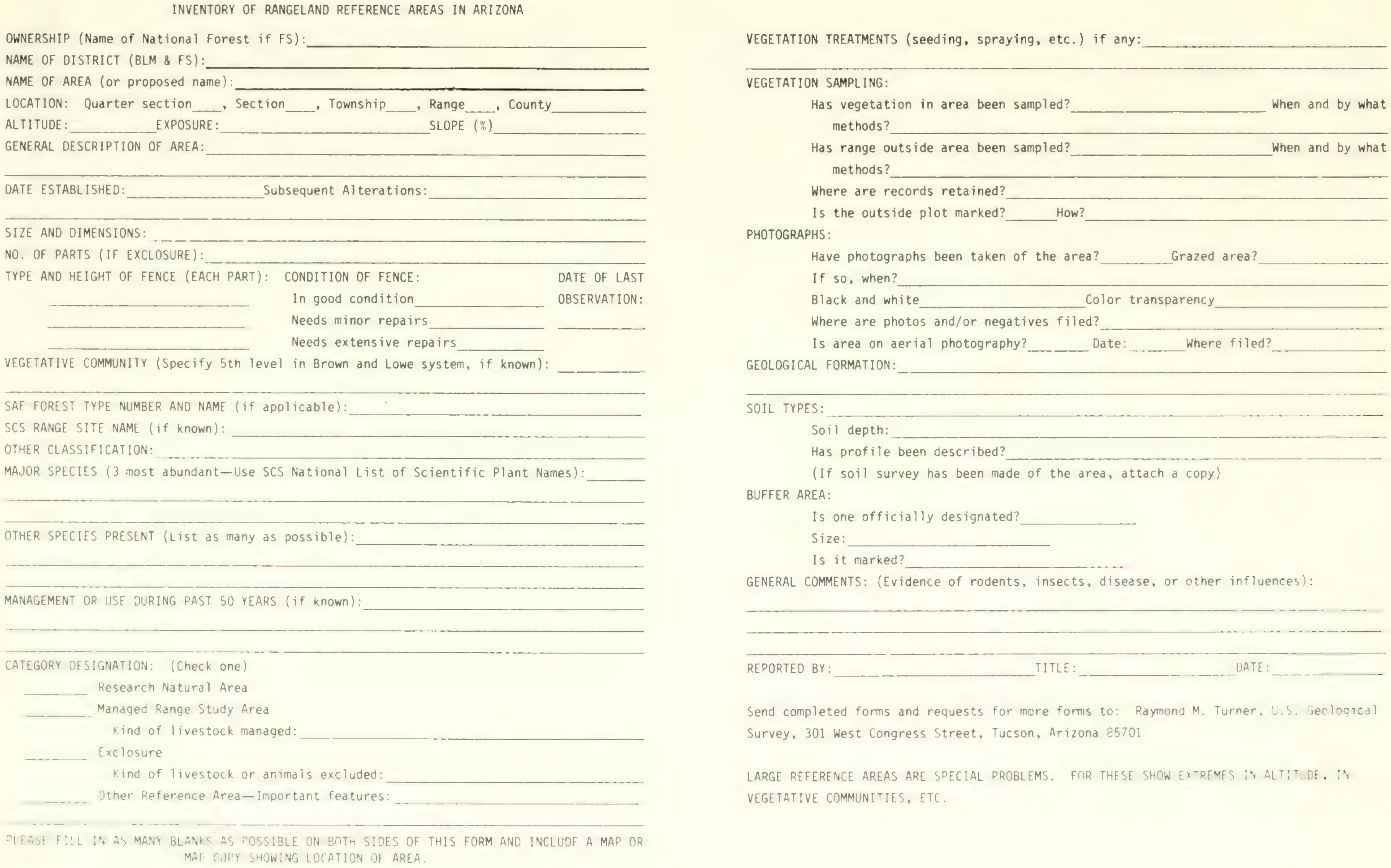


Figure 4.—Three views of Santa Rita Experimental Range Plot No. 14 (Area 200). (a) In 1930, after 9 years of protection the grass is taller inside the plot (left) partly because the grass outside is closely grazed. (b) By 1952, mesquites are larger than before and more numerous on both sides of the fence. The grass outside continues to be heavily grazed. (c) In 1978, a story of grasses intemingles with mesquite on both sides of the fence.



INVENTORY OF RANGELAND REFERENCE AREAS IN ARIZONA

OWNERSHIP (Name of National Forest if FS): ______

NAME OF DISTRICT (BLM & FS): ______

NAME OF AREA (or proposed name): ______

LOCATION: Quarter section ____, Section ____, Township ____, Range ____, County ______

ALTITUDE: ______ EXPOSURE: ______ SLOPE (%) ______

GENERAL DESCRIPTION OF AREA: ______

DATE ESTABLISHED: ______ Subsequent Alterations: ______

SIZE AND DIMENSIONS: ______

NO. OF PARTS (IF EXCLOSURE): ______

TYPE AND HEIGHT OF FENCE (EACH PART):	CONDITION OF FENCE:	DATE OF LAST OBSERVATION:
______	In good condition ______	______
______	Needs minor repairs ______	______
______	Needs extensive repairs ______	

VEGETATIVE COMMUNITY (Specify 5th level in Brown and Lowe system, if known): ______

SAF FOREST TYPE NUMBER AND NAME (if applicable): ______

SCS RANGE SITE NAME (if known): ______

OTHER CLASSIFICATION: ______

MAJOR SPECIES (3 most abundant—Use SCS National List of Scientific Plant Names): ______

OTHER SPECIES PRESENT (List as many as possible): ______

MANAGEMENT OR USE DURING PAST 50 YEARS (if known): ______

CATEGORY DESIGNATION: (Check one)

______ Research Natural Area

______ Managed Range Study Area

Kind of livestock managed: ______

______ Exclosure

Kind of livestock or animals excluded: ______

______ Other Reference Area—Important features: ______

PLEASE FILL IN AS MANY BLANKS AS POSSIBLE ON BOTH SIDES OF THIS FORM AND INCLUDE A MAP OR MAP COPY SHOWING LOCATION OF AREA.

VEGETATION TREATMENTS (seeding, spraying, etc.) if any: ______

VEGETATION SAMPLING:

Has vegetation in area been sampled? ______ When and by what methods? ______

Has range outside area been sampled? ______ When and by what methods? ______

Where are records retained? ______

Is the outside plot marked? ______ How? ______

PHOTOGRAPHS:

Have photographs been taken of the area? ______ Grazed area? ______

If so, when? ______

Black and white ______ Color transparency ______

Where are photos and/or negatives filed? ______

Is area on aerial photography? ______ Date: ______ Where filed? ______

GEOLOGICAL FORMATION: ______

SOIL TYPES: ______

Soil depth: ______

Has profile been described? ______

(If soil survey has been made of the area, attach a copy)

BUFFER AREA:

Is one officially designated? ______

Size: ______

Is it marked? ______

GENERAL COMMENTS: (Evidence of rodents, insects, disease, or other influences): ______

REPORTED BY: ______ TITLE: ______ DATE: ______

Send completed forms and requests for more forms to: Raymond M. Turner, U.S. Geological Survey, 301 West Congress Street, Tucson, Arizona 85701

LARGE REFERENCE AREAS ARE SPECIAL PROBLEMS. FOR THESE SHOW EXTREMES IN ALTITUDE, IN VEGETATIVE COMMUNITIES, ETC.

Figure 5.—Example of form used to report reference area information.

Sequence number.—A number is assigned to index each reference area in the order it appears in the publication.

Name of area.—The name listed is that appearing on the inventory form. In a few cases where no name was supplied, a name was invented based upon some nearby physiographic feature.

Location.—The location for small reference areas is given to the nearest one-fourth section. For large reference areas (e.g., Grand Canyon National Park) no location is given; readers must depend on the map accompanying this report. Some areas of intermediate size are located by one-half section or by township(s) only. In a few instances, where the reference area lies in a portion of Arizona where a cadastral survey has not established township lines, location is given as latitude and longitude under Comments.

County.—The county in which the area is located is noted. For areas that occur in two counties, one is noted under Comments.

Elevation.—Units are in feet. Where areas are large, the range from the lower to the upper elevation is listed.

Vegetation.—This information is given in numeric form. To find the equivalent vegetation community, see appendix 5. The classification system is from Brown and Lowe (1974a, 1974b) and Brown et al. (1979) and uses the numeration in the RUNWILD II Program of the Rocky Mountain Forest and Range Experiment Station and the Southwest Region, USDA Forest Service (Patton 1978). Only one major southwestern biome (alpine tundra) is not represented as a reference area.

Size.—Where known, the size of the reference area is given as area (acres or square miles) or as dimensions (feet or miles).

Date of establishment.—For some areas, the year of establishment is unknown. No date is shown for inaccessible areas.

Vegetation sample.—An agency responsible for a reference area sometimes has vegetation sampling data in its files. If so, access to these data is through the administering agency only.

Photographs.—If an agency has photographs of a reference area in its files, access to these photographs is through the administering agency only.

Animals excluded.—The items appearing here are, in most instances, just as they appeared on the inventory forms. The term "rodent" can be taken to include lagomorphs (rabbits and hares), in most instances.

Comments.—The last statement appearing on some of the entries gives various additional information, including publications listed in the Literature Cited section, that describe the reference area or research conducted in the reference area.

To increase the usefulness of the listing, several appendixes list the reference areas by county, date of establishment, elevation, excluded animals, and vegetative type. Reference areas are indexed by sequence number.

In addition, a map (scale of 1:1,000,000) showing the location of all the areas and the size of the larger areas is enclosed. Each is identified by the sequence number used in the text. In some instances reference areas might be located in the field by use of this map alone; finding most will require a map of larger scale, however.

Before studying exclosures or inaccessible areas, contact the owner or administrative agency first to avoid disturbing studies that may be in progress.

ABBREVIATIONS LIST

AGF	Arizona Game and Fish Department
ARS	Science and Education Administration (formerly Agricultural Research Service)
ASPB	Arizona State Parks Board
BLM	Bureau of Land Management
BTSA	Boyce Thompson Southwest Arboretum
IBP	International Biological Program
LDS	Latter Day Saints
NRA	National Recreation Area
PL	Private land
SAEF	Sierra Ancha Experimental Forest
SCS	Soil Conservation Service
SRER	Santa Rita Experimental Range
UA	University of Arizona
USFS	USDA Forest Service

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REFERENCE AREAS

ARIZONA GAME AND FISH DEPARTMENT

1. Becker Lake: Sec. 19, 20, 29, 30, T9N, R29E; Apache; 7,000 feet; 422.00, 621.00;
    a. 337.75 acres; 1974; cattle.

2. Black Butte Mesquite Bosque: T1S, R4W; Maricopa; 800-870 feet; 233.10, 233.20, 531.70;
    a. 1,191 acres; 1971; photos on file; livestock; area contains virgin bosques of mesquite.

3. Black Canyon Range: Sec. 28, T6N, R2E; Maricopa; 1,500-2,000 feet; 531.10;
    a. 1,709 acres; 1963; cattle; partly in sec. 33.

4. Concho Lake: Sec. 18, T12N, R26E; Apache; 6,000 feet; 422.00, 621.00;
    a. 30 acres; livestock; public fishing site, establishment date unknown.

5. Cunningham Tracts: Sec. 7, 8, 18, T9N, R15E; Gila; 5,968 feet; 221.20, 421.20;
    a. 62.5 acres; 1952; cattle.
    b. 42.5 acres; 1952; cattle.

6. Duran Ranch: Sec. 9, T12N, R14E; Coconino; 7,200 feet; 421.10;
    a. 31.40 acres; cattle; partly in sec. 16, establishment date unknown.

7. Dye Ranch: Sec. 6, T12N, R14E; Coconino; 7,300 feet; 421.10;
    a. 38.03 acres; cattle; partly in sec. 7, establishment date unknown.

8. Fite Property: Sec. 32, T5N, R28E; Apache; 7,660 feet; 621.10;
    a. size unknown; 1972; cattle; partly in sec. 3, 4, 9, T4N, R28E.

9. Hancock Tract Parcel 1: SW1/4 sec. 4, T11N, R19E; Navajo; 6,400 feet; 221.20, 224.10;
    a. 160 acres approx.; livestock; establishment date unknown.

10. Hancock Tract Parcel 2: NE1/4 sec. 9, T11N, R19E; Navajo; 6,400 feet; 221.20, 224.10;
    a. 160 acres approx.; livestock; establishment date unknown.

11. Koger Pasture: Sec. 24, T19N, R11E; Coconino; 5,938-6,310 feet; 224.10, 422.30, 422.40;
    a. 640 acres; 1975; photos on file; bison, cattle; some use by elk and occasionally by stray bison.

12. P.S. Ranch: N1/2 sec. 10, T4N, R28E; Apache; 7,624 feet; 324.00, 621.10;
    a. 160 acres; 1968; cattle; partly in sec. 3.

13. Roper Lake: Sec. 7, 8, T8S, R26E; Graham; 3,100 feet; 233.20, 621.00;
    a. size unknown; 1969; cattle.

14. Texas Hill No. 2: Sec. 30, 31, T6S, R13E; Yuma; 350 feet; 233.20, 531.20;
    a. 80 acres; 1947; cattle.

15. Three Points Range: Sec. 30, 31, T15S, R10E; Pima; 2,500-2,800 feet; 531.10;
    a. 1,281.48 acres; 1968; cattle.

16. Tillman Ranch: Sec. 9, 10, T12N, R14E; Coconino; 7,100 feet; 421.10;
    a. 20.71 acres; cattle; establishment date unknown.

17. Vincent Ranch: Sec. 3, 4, T12N, R13E; Coconino; 7,300 feet; 421.10;
    a. 36.41 acres; cattle; establishment date unknown.

18. Wolfe Ranch: Sec. 18, 19, T12N, R14E; Coconino; 7,400 feet; 421.10;
    a. 31.41 acres; cattle; establishment date unknown.

ARIZONA STATE LAND DEPARTMENT

19. Aravaipa Remote Area: NW1/4 sec. 20, T6S, R19E; Graham; 3,600 feet; 423.10;
    a. 2 acres; vegetation data on file; photos on file; livestock.

20. Big Horn Sheep Inclosure (AGF): SE1/4 sec. 4, T6S, R18E; Pinal; 3,300-4,000 feet; 423.10;
    a. 112 acres; 1957; vegetation data on file; photos on file; livestock; excludes livestock and formerly confined bighorn sheep.

21. Chew Exclosure: NW1/4 sec. 2, T17S, R31E; Cochise; 4,480 feet; 523.20;
    a. 10 acres approx.; 1958; livestock; proposed Natural Area; (Chew and Chew 1965).

22. Coconino Plateau Remote Area: Sec. 16, T26N, R3W; Coconino; 6,000 feet; 224.10;
    a. 5 acres; livestock.

23. Kendall Plot (ARS): SE1/4 sec. 36, T19S, R23E; Cochise; 4,880 feet; 422.10;
    a. one-fourth acre approx.; 1963; vegetation data on file; photos on file; cattle.

24. Kent Smith Wildlife Exclosure (BLM): SE1/4 sec. 10, T18N, R14W; Mohave; 3,200 feet; 522.00;
    a. 300 by 300 feet; 1967; livestock.
    b. 50 by 50 feet; 1967; livestock, deer.
    c. 6 by 6 feet; 1967; livestock, deer, rodents.

25. La Cienega Exclosure (BLM): NE1/4 sec. 6, T16N, R16W; Mohave; 2,840 feet; 522.10;
    a. 300 by 350 feet approx.; 1967; livestock.

26. Lucky Hills Watershed (ARS): NW1/4 sec. 36, T19S, R22E; Cochise; 4,580 feet; 523.20;
    a. 20 acres; 1963; vegetation data on file; photos on file; cattle;
    b. 2.8 acres sprayed with herbicide, seeded to grass, 1975.

27. Montijo Flat (ARS): SW1/4 sec. 31, T19S, R22E; Cochise; 4,200 feet; 523.20;
    a. 2 acres approx.; 1965; cattle, rabbits; shrubs removed, seeded to blue grama.

28. Pacific Western Exclosure (SCS): NE1/4 sec. 28, T9S, R26E; Graham; 3,840 feet; 423.60;
    a. 1 acre; 1936; photos on file; livestock.

29. St. Johns Remote Area: NE1/4 sec. 4, T11N, R29E; Apache; 6,700 feet; 224.10;
    a. 30 acres approx.; livestock.

30. TU8 Plot (ARS): SE 1/4 sec. 32, T19S, R23E; Cochise; 4,670 feet; 423.10;
    a. 1 acre approx.; 1963; vegetation data on file; photos on file; cattle, rabbits.

BUREAU OF LAND MANAGEMENT

Phoenix District

31. Alamo Road: Sec. 34, T10N, R8W; Yavapai; 2,850 feet; 522.10;
    a. 200 by 200 feet; livestock; establishment date unknown.

32. Big Ranch Range Exclosure: NE1/4 sec. 22, T25N, R20W; Mohave; 2,840 feet; 423.20, 522.20;
    a. 213 by 213 feet; 1956; livestock.

33. Blue Tank Exclosure: SE1/4 sec. 12, T19N, R15W; Mohave; 4,640 feet; 323.10;
    a. 278 by 278 feet; 1965; livestock.
    b. 49 by 49 feet; 1965; livestock, deer.

34. Buckskin Exclosure: SW1/4 sec. 7, T10N, R12W; Yuma; 1,600 feet; 531.10;
    a. 200 by 200 feet; 1976; vegetation data on file; photos on file; cattle, burros.

35. Canyon Ranch Exclosure: NW1/4 sec. 20, T24N, R16W; Mohave; 3,155 feet; 423.10;
    a. 300 by 350 feet approx.; 1967; livestock.

36. Constellation Road Exclosure: SW1/4 sec. 27, T8N, R4W; Yavapai; 2,700 feet; 531.10;
    a. 150 by 200 feet; 1976; vegetation data on file; photos on file; cattle.

37. Double Dike Remote Area: NE1/4 sec. 13, T19S, R7E; Pima; 5,750 feet; 225.20;
    a. 40 acres; livestock.

38. End Water Study Plot: NW1/4 sec. 19, T24N, R11W; Mohave; 4,600 feet; 422.10;
    a. 300 by 350 feet approx.; 1967; livestock.

39. Gold Basin Range Exclosure: SE1/4 sec. 26, T27N, R18W; Mohave; 3,200 feet; 522.10;
    a. 213 by 213 feet; 1956; livestock.

40. Hells Canyon Exclosure: NE1/4 sec. 19, T24N, R13W; Mohave; 4,880 feet; 323.10;
    a. 309 by 309 feet; 1965; livestock.
    b. 40 by 40 feet; 1965; livestock, deer.

41. La Cienega Range Exclosure: SE1/4 sec. 36, T16N, R17W; Mohave; 2,760 feet; 522.10;
    a. 213 by 213 feet approx.; 1956; cattle.

42. Lower Hualapai Exclosure: S1/2 sec. 2, T19N, R15W; Mohave; 4,000 feet; 323.10;
    a. 300 by 300 feet; 1965; vegetation data on file; photos on file; cattle.
    b. 20 by 20 feet; 1965; vegetation data on file; photos on file; cattle, deer.

43. Park Exclosure: NW1/4 sec. 12, T10N, R13W; Yuma; 1,300 feet; 531.20;
    a. 200 by 300 feet; 1976; vegetation data on file; photos on file; cattle, burros.

44. Quail Springs Range Exclosure: NE1/4 sec. 10, T23N, R19W; Mohave; 3,360 feet; 423.30;
    a. 213 by 213 feet; 1956; livestock.

45. Rincon Study Plot: NW1/4 sec. 9, T23N, R11W; Mohave; 5,000 feet; 423.10;
    a. 300 by 350 feet; 1970; cattle.

46. Small Mammal Research Site: Sec. 21, T11S, R9E; Pima; 2,200 feet; 531.10;
    a. 640 acres; 1971; livestock; was IBP validation site. In Arizona State Parks Board Natural Area No. 73.

47. Tenny Lower Study Plot: NW1/4 sec. 25, T27N, R16W; Mohave; 2,960 feet; 522.20;
    a. 300 by 350 feet; 1972; livestock.

48. Tenny Upper Study Plot: NE1/4 sec. 19, T28N, R15W; Mohave; 5,320 feet; 224.10;
    a. 300 by 350 feet; 1972; livestock; plot chained, seeded to crested and western wheat grasses.

49. Upper Hualapai Exclosure (AGF): SW1/4 sec. 14, T20N, R15W; Mohave; 6,400 feet; 323.10;
    a. 380 by 306 feet; 1965; livestock.
    b. 50 by 50 feet; 1965; livestock, deer.

50. Upper Music Mountain Exclosure: NE1/4 sec. 6, T26N, R14W; Mohave; 5,440 feet; 323.10;
    a. 328 by 328 feet; 1965; livestock.
    b. 39 by 39 feet; 1965; livestock, deer.

51. Wickenburg-Alamo Area: Sec. 11, T10N, R13W; Yuma; 1,350 feet; 531.20;
    a. 1 acre; 1976; livestock.

Safford District

52. Adams Peak Remote Area: SE1/4 sec. 17, T16S, R22E; Cochise; 5,400 feet; 225.20;
    a. 150 by 80 feet; photos on file; livestock; apparently never grazed by domestic livestock.

53. Antelope Well Seeding Exclosure East: E1/2 sec. 15, T12S, R29E; Cochise; 3,680 feet; 523.20;
    a. 209 by 209 feet; 1966; photos on file; cattle; root plowed and seeded.
    b. Size unknown; 1966; photos on file; cattle, rodents; enclosed in previous plot.
    c. 209 by 209 feet; 1966; photos on file; cattle; untreated.
    d. Size unknown; 1966; photos on file; cattle, rodents; enclosed in previous plot.

54. Antelope Well Seeding Exclosure West: SE1/4 sec. 17, T12S, R29E; Cochise; 3,540 feet; 523.50;
    a. 209 by 209 feet; 1967; photos on file; livestock; seeded to Lehmann lovegrass.
    b. 209 by 209 feet; 1967; photos on file; livestock; untreated.

55. Bear Springs Flat Exclosure North: SE1/4 sec. 18, T6S, R24E; Graham; 2,890 feet; 523.20;
    a. 1 acre; 1971; cattle; root plowed, seeded.
    b. 33 by 33 feet; 1971; cattle, rodents; enclosed in previous plot.

56. Bear Springs Flat Exclosure South: SW1/4 sec. 36, T6S, R23E; Graham; 3,040 feet; 523.20;
    a. 2 acres; 1971; vegetation data on file; photos on file; livestock; root plowed; seeded to Lehmann lovegrass.
    b. 33 by 33 feet; 1971; vegetation data on file; photos on file; cattle, rodents; enclosed in previous plot.
    c. 2 acres; 1971; vegetation data on file; photos on file; livestock; no treatment.
    d. 33 by 33 feet; 1971; vegetation data on file; photos on file; cattle, rodents; enclosed in previous plot.

57. Bitter Creek: Sec. 31, T6S, R32E; Greenlee; 3,750 feet; 423.20;
    a. 1 acre; 1953; livestock.

58. Lee Exclosure: NE1/4 sec. 24, T6S, R23E; Graham; 2,970 feet; 523.20;
    a. 1 acre; 1968; vegetation data on file; photos on file; livestock; root plowed; seeded to Lehmann lovegrass.
    b. 33 by 33 feet; 1968; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.
    c. 1 acre; 1968; vegetation data on file; photos on file; livestock; no treatment.
    d. 33 by 33 feet; 1968; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.

59. Mineral Park Exclosure: NW1/4 sec. 7, T14S, R27E; Cochise; 6,350 feet; 323.10;
    a. 1-1/2 acres; 1962; livestock.

60. New Well Seeding Exclosure East: NE 1/4 sec. 5, T9S, R28E; Graham; 3,300 feet; 523.60;
    a. 1 acre; 1970; vegetation data on file; photos on file; livestock; root plowed; seeded to grass.
    b. size unknown; 1970; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.
    c. 1 acre; 1970; vegetation data on file; photos on file; livestock; undisturbed.
    d. size unknown; 1970; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.

61. New Well Seeding Exclosure West: SW1/4 sec. 25, T8S, R27E; Graham; 3,160 feet; 523.60;
    a. 1 acre; 1970; vegetation data on file; photos on file; livestock; root plowed; seeded to grass.
    b. size unknown; 1970; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.
    c. size unknown; 1970; vegetation data on file; photos on file; livestock, rodents; also enclosed in first plot.

62. Pima Plots: Sec. 10, 11, 15, 16, 21, 22, T6S, R23E; Graham; 3,200 feet; 423.60, 523.20;
    a. 2 square miles; 1963; vegetation data on file; cattle; brush control, seeding.

63. Red Hills Exclosure: NW 1/4 sec. 36, T3S, R23E; Graham; 4,300 feet; 423.10;
    a. 2 acres; 1971; vegetation data on file; photos on file; cattle.
    b. 25 by 25 feet; 1971; vegetation data on file; photos on file; cattle, deer; enclosed in previous plot.

64. Ryan Seeding Exclosure: SE1/4 sec. 7, T11S, R29E; Cochise; 3,400 feet; 523.60;
    a. 209 by 209 feet; 1967; photos on file; livestock; seeded to blue panic and Lehmann lovegrass.
    b. 209 by 209 feet; 1967; photos on file; livestock; untreated.

65. Santa Teresa No. 1: SE1/4 sec.13, T7S, R20E; Graham; 4,700 feet; 423.10;
    a. 200 by 200 feet; 1973; cattle, horses.

66. Santa Teresa No. 2: SE1/4 sec. 11, T7S, R20E; Graham; 4,700 feet; 423.40;
    a. 200 by 200 feet; 1972; livestock; fence cut 1977; grazed.

67. Test Well Exclosure: NW1/4 sec. 4, T11S, R27E; Graham; 3,850 feet; 423.60;
    a. 1 acre; 1936; vegetation data on file; livestock.

68. Timber Draw Reseeding Exclosure: N1/2 sec. 19, T11S, R28E; Graham; 3,600 feet; 423.60;
    a. 209 by 209 feet; 1968; vegetation data on file; photos on file; livestock; root plowed; seeded to Lehmann lovegrass.
    b. size unknown; 1968; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.
    c. 209 by 209 feet; 1968; vegetation data on file; photos on file; livestock; untreated.
    d. size unknown; 1968; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.

69. Van Gausig Exclosure: NW1/4 sec. 21, T10S, R26E; Graham; 4,190 feet; 423.60;
    a. 209 by 209 feet; 1967; vegetation data on file; photos on file; livestock; root plowed; seeded to grass.
    b. size unknown; 1967; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.
    c. 209 by 209 feet; 1967; vegetation data on file; photos on file; livestock; untreated.
    d. size unknown; 1967; vegetation data on file; photos on file; livestock, rodents; enclosed in previous plot.

Strip District

70. Antelope Trail Study Plot: NW1/4 sec. 26, T41N, R9W; Mohave; 4,450 feet; 521.00;
    a. 330 by 330 feet; 1969; livestock.

71. Big Horn Sheep Inclosure: Sec. 24, T40N, R15W; Mohave; 4,000 feet; 522.00;
    a. 1 square mile approx.; 1978; livestock; also in sec. 23, 25; big horn sheep confined within.

72. Big Sage Natural Area: NE1/4 sec. 28, T40N, R1E; Coconino; 5,900 feet; 224.10;
    a. 160 acres; 1972; cattle; adjacent land plowed and seeded; established natural area (BLM).

73. Black Rock Mountain Study Plot: SW1/4 sec. 1, T39N, R14W; Mohave; 6,800 feet; 221.20;
    a. 330 by 330 feet; 1965; livestock.

74. Bundy Study Plot: NW1/4 sec. 21, T35N, R9W; Mohave; 6,250 feet; 2224.10;
    a. 550 by 330 feet; 1965; livestock.

75. Carroll Study Plot: SW1/4 sec. 19, T36N, R9W; Mohave; 6,300 feet; 521.10;
    a. 330 by 330 feet; 1965; livestock.

CLEMSON UNIVERSITY LIBRARY
DOCUMENTS DEPT.

76. Cedar Knoll: SE1/4 sec. 8, T39N, R1W; Coconino; 5,640 feet; 521.10;
    a. 1 acre; 1955; cattle; established between 1950 and 1960.

77. Chamberlain Pugh Study Plot: NW1/4 sec. 20, T39N, R2W; Coconino; 5,200 feet; 521.10;
    a. 330 by 330 feet; 1968; livestock.

78. Cougar Spring Exclosure Fence: Sec. 25, T39N, R15W; Mohave; 6,400 feet; 321.10;
    a. 1 by 1/4 mile; 1965; livestock.

79. Houserock Valley Parker Place: SW1/4 sec. 8, T38N, R4E; Coconino; 5,100 feet; 422.00;
    a. 75 by 75 feet; 1927; cattle; partly disturbed cemetery.

80. Ide Valley Study Plot: NE1/4 sec. 5, T38N, R13W; Mohave; 5,000 feet; 521.10;
    a. 330 by 330 feet; 1965; livestock.

81. Jacob Well Study Plot: NE1/4 sec. 8, T37N, R15W; Mohave; 3,700 feet; 521.30;
    a. 2 acres; 1968; livestock; burned prior to fencing.

82. Low Mountain Study Plot: E1/2 sec. 31, T40N, R13W; Mohave; 6,600 feet; 224.10;
    a. 208 by 416 feet; 1970; livestock;
    b. 104 by 208 feet; 1970; big game.

83. Main Street Study Plot: NE1/4 sec. 15, T38N, R11W; Mohave; 5,000 feet; 422.20;
    a. 330 by 330 feet; 1965; livestock.

84. Maple Spring Exclosure: NW1/4 sec. 20, T39N, R13W; Mohave; 5,800 feet; 224.10;
    a. one-half acre; 1977; livestock; encloses spring.

85. Miller Range and Wildlife Study Plot: NW1/4 sec. 23, T39N, R2W; Coconino; 5,500 feet; 521.10;
    a. 330 by 330 feet; 1968; livestock.

86. Mud Spring Study Plot: SE1/4 sec. 24, T38N, R14W; Mohave; 4,000 feet; 522.00;
    a. 330 by 330 feet; 1971; livestock.

87. Parker Exclosure Fence: Sec. 26, T39N, R10W; Mohave; 4,300 feet; 422.00;
    a. 960 acres; 1952; photos on file; livestock; also in sec. 27, 34, 35.

88. Poverty Mountain Wildlife Exclosure: Sec. 25, T35N, R12W; Mohave; 5,900 feet; 224.10;
    a. 800 by 800 feet; 1976; livestock; parts cleared, plowed, burned, and seeded.

89. Salt Draw Study Plot: SW1/4 sec. 26, T32N, R13W; Mohave; 6,080 feet; 224.10;
    a. 660 by 660 feet; 1965; livestock; seeded to wheat grass.

90. Seegmiller Mt. No. 1 Study Plot: Sec. 5, 6, T39N, R11W; Mohave; 5,400 feet; 224.10;
    a. 330 by 330 feet; 1965; livestock.

91. Seegmiller Mt. No. 2 Study Plot: SE1/4 sec. 25, T40N, R12W; Mohave; 5,700 feet; 224.10;
    a. 330 by 330 feet; 1965; livestock.

92. Soapstone Study Plot: SW1/4 sec. 17, T38N, R12W; Mohave; 5,100 feet; 224.10;
    a. 330 by 330 feet; 1969; livestock.

93. Sunset Study Plot: NE1/4 sec. 7, T38N, R4W; Mohave; 4,850 feet; 321.00;
    a. 325 by 325 feet; 1967; livestock.

94. Temple Trail Study Plot; NW1/4 sec. 23, T38N, R9W; Mohave; 5,540 feet; 422.00;
    a. 330 by 330 feet; 1965; livestock.

95. Trails End Study Plot: SE1/4 sec. 20, T39N, R14W; Mohave; 6,800 feet; 224.10;
    a. 330 by 330 feet; 1967; livestock; includes 20 by 20 feet wildlife exclosure; seeded to wheatgrass.

96. Trumbull Mt. Wildlife Exclosure: SE1/4 sec. 5, T34N, R8W; Mohave; 6,600 feet; 221.20;
    a. 800 by 800 feet; 1976; livestock; plowed and seeded in part.

97. White Rock Soapstone Plot: NE1/4 sec. 12, T38N, R13W; Mohave; 5,200 feet; 224.10;
    a. 330 by 330 feet; 1967; livestock.

98. White Sage YCC Exclosure: Sec. 21, T39N, R1W; Coconino; 5,800 feet; 521.10;
    a. 330 by 330 feet; 1977; livestock.

99. White Tank Seeding Exclosure: Sec. 34, T39N, R12W; Mohave; 5,000 feet; 521.10;
    a. 120 acres; 1949; livestock; seeded to crested wheat grass.

100. Wildcat Study Plot: NE1/4 sec. 5, T33N, R12W; Mohave; 5,800 feet; 521.10;
    a. 330 by 330 feet; 1965; livestock.

101. Woolley Study Plot: NW1/4 sec. 33, T37N, R4E; Coconino; 5,400 feet; 422.00;
    a. 330 by 330 feet; 1971; livestock.

Yuma District

102. Lake Havasu 1: SE1/4 sec. 14, T12N, R19W; Mohave; 640 feet; 531.20;
    a. 231 by 66 feet; 1974; livestock.

103. Lake Havasu 2: SW1/4 sec. 12, T12N, R19W; Mohave; 820 feet; 531.20;
    a. 231 by 66 feet; 1974; livestock.

INDIAN RESERVATIONS

Fort Apache

104. Airport Flats: Sec. 2, T7N, R17E; Gila; 5,200 feet; 422.10, 422.40;
    a. 153 by 137 feet; 1963; vegetation data on file; photos on file; livestock; area burned, root plowed, seeded in 1961.

105. G Wash: SW1/4 sec. 7, NW1/4 sec. 18, T5N, R21E; Gila; 5,120 feet; 422.10;
    a. 309 by 618 feet; 1940; vegetation data on file; photos on file; livestock; juniper cleared south half, 1941.

Papago

106. Black Mountain Remote Area: Sec. 31, T15S, R13E; Pima; 3,500 feet; 531.00;
    a. 70 acres; vegetation data on file; photos on file; cattle, horses; steep mountain with slopes of loose rock; (Ferguson 1950).

MULTIPLE OWNERSHIP

Arizona State Land Department and Private

107. Sombrero Butte Remote Area: NE1/4 sec. 27, T8S, R18E; Pinal; 5,570 feet; 225.20, 423.50;
    a. 120 acres; vegetation data on file; photos on file; cattle; accessible to deer but not livestock.

Arizona State Land Department, Private, and USDA Forest Service

108. The Research Ranch, Inc.: Sec. 13-17, 21-24, 26-28, 34-36, T21S, R18E; Santa Cruz; 4800-5200 feet; 225.20, 422.10, 423.10;
    a. 8,000 acres; 1969; vegetation data on file; photos on file; livestock; (Bahre 1977, Bonham 1972).

Arizona State Land Department and University of Arizona

109. Tumamoc Hill (UA): Sec. 15, T14S, R13E; Pima; 2,369-3,108 feet; 531.10, 531.20;
    a. 869 acres; 1907; vegetation data on file; photos on file; livestock; (Gibble 1950, Martin and Turner 1977, Murray 1959, Shreve 1929, Shreve 1937, Spalding 1909).

Bureau of Land Management and Private

110. Aravaipa Canyon Primitive Area: T6S, R17, 18, 19E; Pinal Co. and Graham Co.; 2,600-3,700 feet; 223.00, 423.00, 531.00;
    a. 5,107 acres; 1969; vegetation data on file; photos on file; livestock.

PRIVATE

111. Canelo Hills Cienega: Sec. 33, T21S, R18E; Santa Cruz; 4,950 feet; 223.20, 225.20;
    a. 165 acres; 1969; livestock; owned by Nature Conservancy.

112. Clarence May Memorial (AGF): Sec. 8, 9, 17, T17S, R31E; Cochise; 5,100 feet; 523.50;
    a. size unknown; 1952; cattle; grazed by horses.

113. Dos Cabezas Cemetery: NE1/4 sec. 31, T14S, R27E; Cochise; 5,050 feet; 423.10;
    a. 4 + acres; 1925; cattle; ungrazed cemetery; 1/3 area disturbed; establishment date approx.

114. Greenlee Country Club: S1/2 sec. 17, T6S, R31E; Greenlee; 3,550 feet; 523.20, 523.50;
    a. 320 acres; 1950; livestock; also includes N1/2 sec. 20, T6S, R31E; partly disturbed.

115. Greenlee County Airport: Sec. 36, T5S, R30E; Greenlee; 3,680 feet; 423.20;
    a. 500 acres; 1940; livestock; partly disturbed.

116. Luna Lake Wildlife Area (AGF): Sec. 17, T5N, R31E; Apache; 8,046 feet; 621.10;
    a. 6.2 acres; cattle.

117. Meteor Crater Remote Area: Sec. 13, 24, T19N, R12E; Coconino; 5,125-5,725 feet; 422.00;
    a. 320 acres; photos on file; livestock.

118. Safford Airport: Sec. 6, T7S, R27E; Graham; 3,158 feet; 423.20;
    a. 600 acres; 1937; photos on file; livestock; date approx.; part of sec. 1, T7S, R26E; partly disturbed.

119. Sonoita Creek: Sec. 11, 12, 13, 14, T22S, R15E; Santa Cruz; 4,000 feet; 223.20, 233.10;
    a. 312 acres; 1966; livestock; owned by Nature Conservancy; (Smith 1974).

120. St. Johns LDS Remote Area: S1/2 sec. 3, T14N, R28E; Apache; 6,000 feet; 224.10;
    a. 200 acres approx.; photos on file; livestock.

U.S. DEPARTMENT OF DEFENSE

121. Fort Huachuca: T22S, R20E; Cochise; 4,000-8,410 feet; 221.00, 225.00, 423.00, 523.00;
   a. 73,000 acres; 1877; photos on file; livestock; most of area ungrazed by livestock since 1949.

USDA FOREST SERVICE

Apache-Sitgreaves National Forest

Alpine Ranger District

122. Browse Exclosure 1 (AGF): SE1/4 sec. 3, T3N, R31E; Greenlee; 6,100 feet; 225.20;
   a. 1 acre; vegetation data on file; cattle; establishment date unknown.

123. Browse Exclosure 2 (AGF): SW1/4 sec. 33, T4N, R31E; Greenlee; 6,700 feet; 225.20;
   a. 1 acre; vegetation data on file; cattle; establishment date unknown.

124. Browse Exclosure 3 (AGF): SW1/4 sec. 27, T4N, R31E; Greenlee; 6,700 feet; 225.20;
   a. 1 acre; vegetation data on file; cattle; establishment date unknown.

125. Campbell Blue Streambottom: Sec. 31, 32, T4N, R32E; Greenlee; 6,550 feet; 223.10;
   a. 1/2 by 1/4 mile; 1935; cattle; fall or spring use by cattle since 1973.

126. Double Cienega Exclosures: NW1/4 sec. 18, T3N, R29E; Greenlee; 9,000 feet; 411.00;
   a. 1 acre; cattle, big game; establishment date unknown.
   b. 1 acre; cattle; establishment date unknown.

127. Grant Creek Fence Plot (AGF): W1/2 sec. 11, T3N, R30E; Greenlee; 6,000 feet; 323.10;
   a. 3 acres; 1960; cattle.

128. Luna Lake Wildlife Area (AGF): Sec. 17, T5N, R31E; Apache; 8,046 feet; 621.10;
   a. 100.8 acres; cattle; establishment date unknown.

129. Red Hill Fence Plot (AGF): NW1/4 sec. 34, T4N, R31E; Greenlee; 6,500 feet; 323.10;
   a. 3 acres; 1960; cattle.

130. State Line Streambottom: SE1/4 sec. 5, T4N, R32E; Greenlee; 6,400 feet; 223.10;
   a. size unknown; 1935; cattle; also in sec. 8; seasonal cattle use since 1973.

131. Swafford Canyon Streambottom: Sec. 5, 24, T4N, R31E; Greenlee; 6,000 feet; 223.10;
   a. 1 by 1/2 mile; 1935; cattle.

132. Upper Blue Spring Streambottom: Sec. 18, T4N, R32E; Greenlee; 6,200 feet; 223.10;
   a. size unknown; 1935; cattle; also in three adjacent sections; seasonal cattle use since 1973.

Clifton Ranger District

133. Coal Creek: NE1/4 sec. 9, T4S, R32E; Greenlee; 5,720 feet; 221.20;
   a. 95 by 91 feet; 1926; cattle.

134. Eagle Administrative Study Plot; NW1/4 sec. 19, T1S, R29E; Greenlee; 5,840 feet; 422.10;
   a. 75 by 75 feet; 1926; photos on file; cattle.

135. East Eagle Exclosure: NE1/4 sec. 4, T2N, R28E; Greenlee; 7,000 feet; 225.20;
   a. 3 acres; 1961; vegetation data on file; photos on file; cattle, big game.
   b. 3 acres; 1961; vegetation data on file; photos on file; cattle.

136. Juan Miller Range Study Plot: NW1/4 sec. 9, T2S, R29E; Greenlee; 6,120 feet; 224.10;
   a. 50 by 75 feet; 1928; photos on file; cattle.

137. Maple Peak Range Study Plot: SW1/4 sec. 2, T1S, R31E; Greenlee; 6,400 feet; 225.20;
   a. 75 by 75 feet; 1931; photos on file; cattle.
   b. 75 by 75 feet; 1931; photos on file; cattle, deer.

138. Strayhorse Exclosure: NE1/4 sec. 14, T2N, R29E; Greenlee; 7,700 feet; 221.20;
   a. 650 by 150 feet; 1965; photos on file; cattle; evidence of slight cattle use.

Pinedale Ranger District

139. Potato Patch (AGF): SE1/4 sec. 24, T11N, R17E; Navajo; 6,800 feet; 221.00, 421.00;
   a. 5 acres; 1958; cattle.

Springerville Ranger District

140. Basin Lake: NW1/4 sec. 18, T6N, R28E; Apache; 9,100 feet; 411.00;
   a. 82 acres; 1936; vegetation data on file; photos on file; cattle; cattle completely excluded 1978; grazed rarely before.

141. Beehive: NW1/4 sec. 19, T8N, R27E; Apache; 9,300 feet; 411.00;
   a. one-fourth acre approx.; livestock, deer, elk; establishment date unknown.
   b. one-fourth acre approx.; livestock; establishment date unknown.

142. Crosby Crossing: Sec. 13, T6N, R28E; Apache; 8,800 feet; 411.00;
    a. 34 acres; 1938; cattle.

143. Sheep Springs: Sec. 31, T8N, R27E; Apache; 9,200 feet; 411.00;
    a. 100 by 100 feet; 1924; vegetation data on file; photos on file; sheep.

144. Udall Spring: SE1/4 sec. 9, T8N, R26E; Apache; 9,400 feet; 411.00;
    a. 50 by 100 feet; cattle; establishment date unknown.

145. Water Canyon: Sec. 28, T8N, R29E; Apache; 7,300 feet; 422.10;
    a. 70 by 100 feet; 1939; vegetation data on file; cattle, horses.

Coconino National Forest

Beaver Creek Ranger District

146. Cedar Mountain: Sec. 28, T14N, R6E; Yavapai; 4,000 feet; 423.60;
    a. size unknown; 1940; livestock; fence reconstructed in 1966.

147. Mud Tanks: SW1/4 sec. 25, T13N, R7E; Yavapai; 6,000 feet; 224.10;
    a. 660 by 330 feet; 1949; livestock; plot reseeded to grasses; area plowed.

148. School House Draw Plot: NW1/4 sec. 20, T15N, R6E; Yavapai; 3,900 feet; 423.50;
    a. 1 acre; 1930; cattle, horses.

149. V Bar V Plot: SW1/4 sec. 9, T14N, R6E; Yavapai; 3,880 feet; 423.50;
    a. 205 by 205 feet; vegetation data on file; photos on file; livestock; established before 1940.

Blue Ridge Ranger District

150. Fred Haught Remote Area: E1/2 sec. 31, T13N, R11E; Coconino; 7,300 feet; 221.20;
    a. 200 acres; livestock; 200-foot high sandstone mesa.

151. Jumbo Pasture Remote Area: Sec. 35, T14N, R10E; Coconino; 7,000 feet; 221.20;
    a. 160 acres; livestock.

Flagstaff Ranger District

152. Cedar Ranch - Highway 180: NW1/4 sec. 16, T25N, R5E; Coconino; 7,200 feet; 224.10;
    a. 100 by 100 feet; 1957; cattle; establishment may be before 1957.

153. Hochderffer Aspen Regeneration Plot: SE1/4 sec. 9, T22N, R6E; Coconino; 8,300 feet; 221.20;
    a. 2.5 acres; 1966; photos on file; cattle.

154. Intersection of Road 231 and Road 75: NE1/4 sec. 13, T20N, R5E; Coconino; 7,200 feet; 221.20;
    a. 450 by 150 feet; cattle, sheep; establishment date unknown, but before 1968.

155. Road 526 Area: NE1/4 sec. 1, T20N, R5E; Coconino;,7,200 feet; 421.10;
    a. 450 by 200 feet; 1967; cattle; establishment date approximate.

Mormon Lake Ranger District

156. Black Springs: Sec. 8, T20N, R7E; Coconino; 6,900 feet; 221.20;
    a. size unknown; 1912; vegetation data on file; photos on file; livestock; fence needs extensive repairs.

157. Double Springs: SW1/4 sec. 14, T18N, R8E; Coconino; 7,500 feet; 221.20;
    a. 10.7 acres; vegetation data on file; photos on file; livestock; establishment date unknown.

158. Schnebley Hill: SE1/4 sec. 35, T18N, R6E; Coconino; 6,000 feet; 224.10;
    a. 100 by 100 feet; 1940; cattle.

Sedona Ranger District

159. Beaverhead: SE1/4 sec. 25, T16N, R5E; Yavapai; 4,500 feet; 224.10;
    a. 50 by 50 feet; 1935; cattle.

160. Dry Creek: SE1/4 sec. 33, T18N, R5E; Yavapai; 4,600 feet; 224.10;
    a. 12.5 acres; 1950; vegetation data on file; photos on file; livestock.

161. Dutch Kid Study Plot: NW1/4 sec. 28, T17N, R6E; Yavapai; 3,800 feet; 423.50;
    a. size unknown; 1962; vegetation data on file; photos on file; cattle.

162. Oak Creek: Sec. 19, T17N, R5E; Yavapai; 4,400 feet; 224.10;
    a. 1 acre approx.; 1940; vegetation data on file; photos on file; livestock.

163. Schuerman Mt.: SE1/4 sec. 16, T17N, R5E; Yavapai; 4,440 feet; 224.10;
    a. 1 acre; 1940; livestock.

164. White Hills: SE1/4 sec. 19, T17N, R4E; Yavapai; 4,100 feet; 423.00;
    a. 10 acres; 1935; vegetation data on file; photos on file; livestock.

165. Windmill: NW1/4 sec. 6, T17N, R5E; Yavapai; 4,400 feet; 423.00;
    a. 30 by 30 feet; 1930; cattle.

Coronado National Forest

Douglas Ranger District

166. Barfoot (AGF): SE1/4 sec. 29, T17S, R30E; Cochise; 8,500 feet; 421.00;
    a. 3 acres; 1957; cattle, deer; fence needs extensive repairs.

167. Halfmoon Game Exclosure K-2: NW1/4 sec. 17, T17S, R23E; Cochise; 5,200 feet; 225.20;
    a. 2.5 acres; 1965; vegetation data on file; photos on file; cattle, deer.
    b. 5 acres; 1965; vegetation data on file; photos on file; cattle.

168. Hands Pass Exclosure (AGF): E1/2 sec. 32, T16S, R30E; Cochise; 6,650 feet; 225.20;
    a. 3 acres; 1957; cattle.
    b. 3 acres; 1957; cattle, deer.

169. NE of Winkler Ranch (AGF): SW1/4 sec. 21, T19S, R29E; Cochise; 5,500 feet; 225.20;
    a. 3 acres; 1957; cattle, deer.

170. Pinery Canyon Administrative Study: SE1/4 sec. 18, T17S, R30E; Cochise; 6,000 feet; 225.10;
    a. 175 by 300 feet; 1930; cattle.

171. Rucker Administrative Study; SE1/4 sec. 22, T19S, R29E; Cochise; 5,700 feet; 225.20;
    a. 400 by 125 feet approx.; 1939; vegetation data on file; cattle; fence needs extensive repairs.

172. Rucker Station (AGF): SE1/4 sec. 14, T19S, R29E; Cochise; 5,800 feet; 323.10;
    a. 3 acres; 1957; cattle, deer.

173. Upper Cave Creek (AGF): SW1/4 sec. 26, T17S, R30E; Cochise; 7,800 feet; 225.10;
    a. 3 acres; 1957; cattle, deer.

Nogales Ranger District

174. Alamo: SE1/4 sec. 35, T23S, R13E; Santa Cruz; 3,780 feet; 423.50;
    a. 150 by 150 feet; 1945; photos on file; cattle.

175. Aliso Springs Riparian Exclosure: SE1/4 sec. 22, T21S, R12E; Santa Cruz; 4,000 feet; 223.10, 225.20;
    a. 40 acres; 1978; cattle.

176. Canoa: SW1/4 sec. 5, T22S, R9E; Pima; 4,600 feet; 423.50;
    a. 75 by 75 feet; 1963; photos on file; cattle; seeded to Lehmann lovegrass.

177. Cedar Dam Riparian Exclosure: NE1/4 sec. 25, T21S, R11E; Pima; 4,100 feet; 223.20;
    a. 40 acres; 1978; cattle.

178. Cedar Tank Riparian Exclosure: SW1/4 sec. 23, T21S. R11E; Pima; 3,800 feet; 223.10;
    a. 40 acres; 1978; cattle.

179. Fresnal: NW1/4 sec. 4, T23S, R9E; Pima; 4,600 feet; 423.10;
    a. 100 by 150 feet; photos on file; cattle; establishment date unknown.

180. Hog Canyon Study Plot: SE1/4 sec. 21, T20S, R16E; Santa Cruz; 4,700 feet; 225.20;
    a. 150 by 200 feet approx.; 1940; vegetation data on file; photos on file; cattle, horses.

181. Lopez Range Study Plot: NW1/4 sec. 14, T20S, R16E; Santa Cruz; 4,940 feet; 422.10;
    a. 45 by 54 feet; 1930; photos on file; cattle.
    b. 45 by 54 feet; 1930; photos on file; cattle.
    c. 150 by 150 feet; 1940; photos on file; cattle.

182. Mesquite Control Project: SW1/4 sec. 21, T23S, R13E; Santa Cruz; 3,700 feet; 423.30;
    a. 2,640 by 300 feet; 1943; photos on file; cattle; light winter use by horses.

183. Montana Dam Riparian Exclosure: SE1/4 sec. 7, T23S, R11E; Pima; 4,000 feet; 223.20;
    a. 40 acres; 1978; cattle.

184. Pena Blanca Canyon: Sec. 26, T23S, R12E; Santa Cruz; 4,500 feet; 233.00;
    a. 400 acres; 1978; cattle.

185. SRER Plot 1: NE1/4 sec. 8, T19S, R15E; Pima; 4,100 feet; 423.00;
    a. 55 by 170 feet; 1916; vegetation data on file; photos on file; cattle; enlarged to present size in 1935.

186. SRER Plot 1A (Rodent): NW1/4 sec. 2, T19S, R14E; Pima; 3,560 feet; 423.00;
    a. 600 by 310 feet; 1918; vegetation data on file; photos on file; cattle.
    b. 270 by 155 feet; 1918; vegetation data on file; photos on file; cattle, rabbits.
    c. 270 by 155 feet; 1918; vegetation data on file; photos on file; cattle, rabbits; (Glendening 1952).

187. SRER Plot 2B (Eriopoda): SE1/4 sec. 30, T18S, R15E; Pima; 3,760 feet; 423.00;
    a. 298 by 300 feet; 1918; vegetation data on file; photos on file; cattle.
    b. 298 by 300 feet; 1925; vegetation data on file; photos on file; cattle.
    c. 50 by 50 feet; 1932; vegetation data on file; photos on file; cattle.

188. SRER Plot 3: NE1/4 sec. 6, T19S, R15E; Pima; 3,850 feet; 423.00;
   a. 75 by 200 feet; 1918; vegetation data on file; photos on file; cattle; enlarged to present size in 1936.

189. SRER Plot 3C (Jack Rabbit): NW1/4 sec. 29, T18S, R15E; Pima; 3,760 feet; 423.00;
   a. 215 by 215 feet; 1918; vegetation data on file; cattle, rabbits.
   b. 66 by 66 feet; 1918; vegetation data on file; cattle, rodents.
   c. 66 by 149 feet; 1918; vegetation data on file; cattle.
   d. 26 by 65 feet; 1918; vegetation data on file; cattle; rabbits.

190. SRER Plot 4: NE1/4 sec. 34, T18S, R14E; Pima; 3440 feet; 423.00;
   a. 136 by 88 feet; 1916; vegetation data on file; cattle; enlarged to present size in 1935.

191. SRER Plot 5: NW1/4 sec. 35, T18S, R14E; Pima: 3,480 feet; 423.00;
   a. 44 by 146 feet; 1916; vegetation data on file; cattle; enlarged to present size in 1935.

192. SRER Plot 6: SW1/4 sec. 32, T18S, R15E; Pima; 3,880 feet; 423.00;
   a. 300 by 65 feet; 1916; vegetation data on file; cattle; enlarged to present size in 1935.

193. SRER Plot 7 (Huerfano): NW1/4 sec. 21, T18S, R15E; Pima; 3,860 feet 423.00;
   a. 220 by 72 feet; 1917; vegetation data on file; photos on file; cattle; enlarged several times to present size, last in 1932.

194. SRER Plot 8: NE1/4 sec. 33, T18S, R15E; Pima; 4,360 feet; 423.00;
   a. 88 by 125 feet; 1917; vegetation data on file; photos on file; cattle; enlarged in 1935; burned in 1959.

195. SRER Plot 9: NW1/4 sec. 14, T19S, R14E; Pima; 3,700 feet; 423.00;
   a. 71 by 73 feet approx.; 1917; vegetation data on file; photos on file; cattle; enlarged to present size in 1936.

196. SRER Plot 10: NE1/4 sec. 23, T19S, R14E; Pima; 3,900 feet; 423.00;
   a. 75 by 150 feet; 1917; vegetation data on file; cattle; enlarged to present size in 1935.

197. SRER Plot 11 (White House): NW1/4 sec. 23, T19S, R14E; Pima; 3,900 feet; 423.00;
   a. 75 by 150 feet; 1918; vegetation data on file; photos on file; cattle; enlarged to present size in 1932.

198. SRER Plot 12 (Northwest Station): NW1/4 sec. 33, T17S, R14E; Pima; 2,960 feet; 423.00;
   a. 117 by 207 feet; 1916; vegetation data on file; photos on file; cattle; enlarged to present size in 1935.

199. SRER Plot 13: NE1/4 sec. 19, T19S, R15E; Pima; 4,180 feet; 423.00;
   a. 101 by 126 feet; 1921; vegetation data on file; photos on file; cattle; enlarged to present size in 1932; (Caraher 1970).

200. SRER Plot 14 (Forest Station): N1/2 sec. 19, T19S, R15E; PIMA; 4,180 feet; 423.00;
   a. 291 by 107 feet; 1921; vegetation data on file; photos on file; cattle; original seven plots rebuilt in 1931.

201. SRER Plot 15: NE1/4 sec. 13, T19S, R14E; Pima; 4,000 feet; 423.00;
   a. 150 by 150 feet; 1916; vegetation data on file; photos on file; cattle; original 60 by 60-foot plot enlarged in 1935; (Caraher 1970).

202. SRER Plot 16: NW1/4 sec. 11, T19S, R14E; Pima; 3,640 feet; 423.00;
   a. 75 by 100 feet; 1921; vegetation data on file; cattle; enlarged to present size in 1936.

203. SRER Plot 17 (Road Station): NW1/4 sec. 11, T19S, R14E; Pima; 3,640 feet; 423.00;
   a. 187 by 324 feet; 1921; vegetation data on file; photos on file; cattle; orginally established as eight plots; refenced in 1932.

204. SRER Plot 18: NE1/4 sec. 4, T19S, R15E; Pima; 4,280 feet; 423.00;
   a. 82 by 164 feet; 1918; vegetation data on file; photos on file; cattle; enlarged in 1932 and 1935.

205. SRER Plot 20: NE1/4 sec. 33, T18S, R14E; Pima; 3,280 feet; 423.00;
   a. 75 by 50 feet; 1916; vegetation data on file; photos on file; cattle; original plot enlarged in 1935 or 1936.

206. SRER Plot 21: NE1/4 sec. 13, T19S, R14E; Pima; 3,920 feet; 423.00;
   a. 75 by 150 feet; 1916; vegetation data on file; cattle; original 60 by 60-foot plot enlarged in 1935. (Caraher 1970).

207. SRER Plot 22: NE1/4 sec. 16, T18S, R15E; Pima; 3,850 feet; 423.00;
   a. 60 by 200 feet approx.; 1916; vegetation data on file; photos on file; cattle; enlarged in 1935 or 1936.

208. SRER Plot 23 (Box Station): SW1/4 sec. 5, SE1/4 sec. 6, T19S, R15E; Pima; 3,920 feet; 423.00;
    a. 286 by 312 feet; 1922; photos on file; cattle.
    b. 286 by 312 feet; 1922; photos on file; cattle.
    c. 286 by 312 feet; 1922; photos on file; cattle; all plots rebuilt in 1932.

209. SRER Plot 24: NE1/4 sec. 19, T18S, R15E; Pima; 3,620 feet; 423.00;
    a. 0.3 acre; 1916; vegetation data on file; cattle.

210. SRER Plot 27 (Mesa Station): SW1/4 sec. 1, T19S, R14E; Pima; 3,700 feet; 423.00;
    a. 75 by 362 feet; 1925; photos on file; cattle; had three parts with deferred grazing until 1936.
    b. 50 by 112 feet; 1936; photos on file; cattle.

211. SRER Plot 28 (Foothill Station): NE1/4 sec. 8, T19S, R15E; Pima; 4,100 feet; 423.00;
    a. 100 by 362 feet; 1925; vegetation data on file; photos on file; cattle; several original plots rebuilt as one plot in 1935.
    b. 25 by 150 feet; 1935; vegetation data on file; photos on file; cattle.

212. SRER Plot 29 (Southwest Station): SE1/4 sec. 33, T18S, R14E; Pima; 3,340 feet; 423.00;
    a. 64 by 180 feet; 1925; vegetation data on file; photos on file; cattle.
    b. 64 by 120 feet; 1925; vegetation data on file; photos on file; cattle.
    c. 64 by 120 feet; 1925; vegetation data on file; photos on file; cattle; nine original plots rebuilt as three plots in 1932.

213. SRER Plot 31 (Parker Station): NE1/4 sec. 17, T19S, R15E; Pima; 4,340 feet; 423.00;
    a. 50 by 100 feet; 1931; vegetation data on file; photos on file; cattle; 1/2 plot formerly a rodent exclosure.
    b. 50 by 50 feet; 1931; vegetation data on file; photos on file; cattle.
    c. 39 by 148 feet; 1935; vegetation data on file; photos on file; cattle; fertilizer experiment plot.

214. SRER Plot 32 (West Station): NW1/4 sec. 30, T18S, R14E; Pima; 3,040 feet; 423.00;
    a. 72 by 72 feet; 1930; photos on file; cattle.

215. SRER Plot 33 (Desert Grassland): NE1/4 sec. 13, T19S, R14E; Pima; 3,860 feet; 423.00;
    a. 7 acres approx.; 1931; photos on file; cattle; old exclosures inside; part burned in 1965.
    b. 100 by 65 feet; 1931; photos on file; cattle; plot has an additional 25 by 25-foot section; (Brown 1950, Cable 1965).

216. SRER Plot 34 (Burroweed): SE1/4 sec. 4, T19S, R14E; Pima; 3,400 feet; 423.00;
    a. 164 by 328 feet; 1932; vegetation data on file; photos on file; cattle; half of plot burned in 1932.
    b. 50 by 50 feet; 1932; vegetation data on file; photos on file; cattle.

217. SRER Plot 35 (Isolation Transect): SW1/4 sec. 35, T18S, R14E; Pima; 3,520 feet; 423.00;
    a. 131 by 787 feet; 1932; vegetation data on file; photos on file; cattle; one-half plot formerly rodent proof.

218. SRER Plot 36: NW1/4 sec. 30, T18S, R14E; Pima; 3,040 feet; 423.00;
    a. 98 by 297 feet; 1934; photos on file; cattle; burroweed control tests.

219. SRER Plot 37: SE1/4 sec. 3, T19S, R14E; Pima; 3,540 feet; 423.00;
    a. 203 by 300 feet; 1934; vegetation data on file; photos on file; cattle; burroweed control tests.

220. SRER Plot 38: NE1/4 sec. 28, T18S, R15E; Pima; 4,120 feet; 423.00;
    a. 98 by 292 feet; 1934; photos on file; cattle; burroweed control tests.

221. SRER Plot 39: NE1/4 sec. 17, T19S, R15E; Pima; 4,300 feet; 423.00;
    a. 39 by 148 feet; 1935; photos on file; cattle.

222. SRER Plot 40: NE1/4 sec. 29, T18S, R15E; Pima; 3,880 feet; 423.00;
    a. 78 by 78 feet; 1935; cattle.

223. SRER Plot 41: NE1/4 sec. 16, T19S, R14E; Pima; 3,560 feet; 423.00;
    a. 325 by 189 feet; 1935; photos on file; cattle; seeded to Lehmann lovegrass before 1946.

224. SRER Plot 42 (Boothill Sta.): SW1/4 sec. 1, T19S, R14E; Pima; 3,700 feet; 423.00;
    a. 60 by 180 feet; 1935; vegetation data on file; photos on file; cattle; rodent exclosure no longer intact.
    b. 60 by 100 feet; 1935; vegetation data on file; photos on file; cattle.
    c. 200 by 40 feet; 1935; vegetation data on file; photos on file; cattle.
    d. 60 by 80 feet; 1935; vegetation data on file; photos on file; cattle.

225. SRER Plot 43(Water Retention): SW1/4 sec.11, T19S, R14E; Pima; 3,660 feet; 423.00;
    a. 900 by 186 feet; 1935; vegetation data on file; photos on file; cattle; application of artificial rain; seeded in 1940.

226. SRER Plot 44 (Gravelly Ridge): W1/2 sec. 30, T18S, R14E; Pima; 3,040 feet; 423.00;
  a. 3,075 by 200 feet; 1934; vegetation data on file; photos on file; cattle.
  b. 3,075 by 200 feet; 1934; vegetation data on file; photos on file; cattle; some seeding and transplanting in both plots. (Barr 1955).

227. SRER Plot 45: SE1/4 sec. 36, T18S, R14E; Pima; 3,720 feet; 423.00;
  a. 46.2 acres; 1935; vegetation data on file; photos on file; cattle; water spreading area; (Thatcher and Hart 1974).

228. SRER Plot 129 (Northeast): SW1/4 sec. 32, T17S, R15E; Pima; 3,300 feet; 423.00;
  a. 60 by 80 feet approx.; 1938; vegetation data on file; photos on file; cattle.

229. SRER Plot 130: NE1/4 sec. 1, T19S, R14E; Pima; 3,800 feet; 423.00;
  a. 640 by 640 feet; 1938; vegetation data on file; photos on file; cattle.
  b. 300 by 325 feet; 1938; vegetation data on file; photos on file; cattle; formerly rodent exclosure; hardware cloth badly damaged.
  c. 325 by 350 feet; 1938; vegetation data on file; photos on file; cattle; (Tiedemann 1970).

230. SRER Plot 131: NW1/4 sec. 10, T19S, R14E; Pima; 3,700 feet; 423.00;
  a. 660 by 660 feet; 1938; vegetation data on file; photos on file; cattle.
  b. 330 by 330 feet; 1938; vegetation data on file; photos on file; cattle; formerly rodent exclosure.
  c. 330 by 330 feet; 1938; vegetation data on file; photos on file; cattle; (Tiedemann 1970).

231. SRER Plot 205: NW1/4 sec. 31, T18S, R15E; Pima; 3,740 feet; 423.00;
  a. 420 by 600 feet; 1946; vegetation data on file; photos on file; cattle; artificial seeding; burned in 1956; (Cable 1961).

232. SRER Plot 280: SE1/4 sec. 31, 32, T18S, R14E; Pima; 3,180 feet; 423.00;
  a. 800 by 1,000 feet; 1965; vegetation data on file; photos on file; cattle; four-wing saltbush vs. mesquite study; (Cable 1972).

233. SRER Plot 286 (NE Exclosure): Sec. 34, T17S, R15E; Pima; 3,400-3,800 feet; 423.00;
  a. 1 by 1-3/4 mile; 1967; photos on file; cattle; also in sec. 3, T18S.

234. SRER Plot 295 (IBP): T18S, R14E; Pima; 3,100-3,260 feet; 423.00;
  a. 200 acres; 1970; vegetation data on file; photos on file; cattle; no treatment.
  b. 200 acres; 1970; vegetation data on file; photos on file; cattle; diesel oil applied to mesquite.
  c. 200 acres; 1970; photos on file; cattle; no treatment.
  d. 200 acres; 1970; photos on file; cattle; mesquite chained; shrub control plots, 1976.
  e. 12.5 acres; 1974; photos on file; cattle, rodents; enclosed in first plot; (Tschirley and Martin 1961).

235. SRER Plot 302: SE1/4 sec. 33, SW1/4 sec. 34, T18S, R15E; Pima; 4,360-4,800 feet; 423.00;
  a. 160 acres; 1972; cattle.

Safford Ranger District

236. CN Ranch: Sec. 7, T10S, R25E; Graham: 5,200 feet; 225.20;
  a. 240 by 178 feet; 1939; vegetation data on file; cattle.

237. Gillespie: NW1/4 sec. 18, T10S, R26E; Graham; 4,300 feet 423.50;
  a. 220 by 225 feet; 1939; vegetation data on file; photos on file; cattle.

238. Pinaleno Mountains: Graham; 5,000-10,500 feet; 211.00, 221.00, 222.00, 223.00, 225.00;
  a. size unknown; livestock; recreation area.

239. Pitchfork: Sec. 2, T10S, R24E; Graham; 5,000 feet; 423.50;
  a. 150 by 250 feet; 1939; vegetation data on file; cattle.

240. Stockton Pass Recreation Area: SW1/4 sec. 1, T10S, R24E; Graham; 5,000 feet; 225.20;
  a. 12 acres approx.; 1966; livestock.

241. Stockton Pass Wildlife Exclosure: NW1/4 sec. 13, T10S, R24E; Graham; 5,800 feet; 225.20;
  a. 2.5 acres; 1963; vegetation data on file; cattle, deer.
  b. 5 acres; 1963; vegetation data on file; cattle.

Santa Catalina Ranger District

242. Ash Creek: T15S, R18E; Pima; 4,000 feet; 233.00;
  a. 6 by 0.5 miles; 1977; cattle.

243. Butterfly Peak Natural Area: T11S, R16E; Pima; 5,000-7,000 feet; 212.00, 221.00, 223.00, 225.00;
  a. 1,000 acres; 1935; photos on file; livestock; unfenced; light grazing by cattle.

244. Pusch Ridge Wilderness Area: Pima; 3,000-9,100 feet; 211.00, 212.00, 221.00, 222.00, 223.00, 225.00, 233.00, 423.00, 531.00;
  a. 56,480 acres; vegetation data on file; photos on file; livestock.

245. Santa Catalina Natural Area: T11S, R15E; Pima; 5,600-8,800 feet; 221.00, 223.00, 225.00;
    a. 4,131 acres; 1927; vegetation data on file; photos on file; livestock; first Natural Area in U.S. for primarily scientific study; (Cheatham et al. 1977).

Sierra Vista Ranger District

246. Lone Mountain: NW1/4 sec. 3, T24S, R19E; Cochise; 5,550 feet; 422.10; 1935; vegetation data on file; photos on file; livestock; untreated.
    a. size unknown; 1963; vegetation data on file; photos on file; livestock;
    b. size unknown; soil surface ripped in 1963.

247. Lower Parker Canyon: Sec. 18, T23S, R19E; Santa Cruz; 4,400 feet; 233.00;
    a. 2.5 by 0.5 mile; 1975; photos on file; cattle.

248. O'Donnell Creek Exclosure: NW1/4 sec. 33, T21S, R18E; Santa Cruz; 4,875 feet; 223.20, 225.20;
    a. 2,000 by 250 feet; 1978; cattle; between Canelo Hills Cienega and the Research Ranch.

249. Vaughn Study Plot: NW1/4 sec. 31, T21S, R18E; Santa Cruz; 5,200 feet; 225.20;
    a. 208 by 208 feet; 1925; vegetation data on file; photos on file; cattle, horses.

250. Vaughn Wildlife Plot: SW1/4 sec. 35, T21S, R17E; Santa Cruz; 5,350 feet; 323.10;
    a. 342 by 247 feet; 1965; vegetation data on file; photos on file; cattle, deer.
    b. 495 by 335 feet; 1965; vegetation data on file; photos on file; cattle.

Kaibab National Forest

Chalender Ranger District

251. Bellemont Allotment Study Plot: NE1/4 sec. 3, T21N, R4E; Coconino; 6,870 feet; 422.10;
    a. 300 by 300 feet; 1940; vegetation data on file; photos on file; cattle, sheep; newly fenced in 1965.

252. Potato Hill Plot: Sec. 11, T24N, R4E; Coconino; 6,860 feet; 422.10;
    a. 300 by 300 feet; 1929; vegetation data on file; photos on file; cattle.

253. Spring Valley Study Plot: NW1/4 sec. 23, T23N, R4E; Coconino; 7,300 feet; 221.20;
    a. 300 by 300 feet; 1940; vegetation data on file; photos on file; cattle.

North Kaibab Ranger District

254. Buck Farm Push: NE1/4 sec. 11, T34N, R4E; Coconino; 6,000 feet; 224.10;
    a. 50 by 50 feet; 1970; bison; juniper cleared; grazed by bison before 1970.

255. Castle Canyon Study Area: NW1/4 sec. 28, T36N, R2E; Coconino; 8,500 feet; 421.10;
    a. 5 acres; 1959; vegetation data on file; cattle; some cattle use; seeded in 1959, 1960, 1961, and 1962.

256. East Rim Study Plot: SW1/4 sec. 21, T35N, R3E; Coconino; 8,800 feet; 211.20;
    a. 1/4 acre; 1931; vegetation data on file; photos on file; cattle, deer.
    b. 4-3/4 acres; 1931; vegetation data on file; photos on file; cattle.

257. Horse Spring Cow Exclosure: NW1/4 sec. 6, T37N, R2W; Coconino; 5,800 feet; 224.10;
    a. 80 acres; 1954; cattle; chemical control of juniper.

258. Saddle Mountain Remote Area: T34N, R5E; Coconino; 6,200-8,400 feet; 224.10;
    a. 5 square miles; photos on file; livestock; also in T34N, R4E; heavy winter deer use until 1967.

259. Sowats Road.: NW1/4 sec. 27, T36N, R2W; Coconino; 6,300 feet; 224.10;
    a. 25 by 25 feet; 1931; cattle.
    b. 25 by 25 feet; 1931; cattle, deer; juniper cleared; fence needs repairs in both plots.

260. Sowats Ridge No. 46: NE1/4 sec. 29, T36N, R2W; Coconino; 6,200 feet; 224.10;
    a. 80 acres; 1931; cattle, deer; fence needs repairs.

261. Table Rock Push Deer Exclosure: NW1/4 sec. 27, T38N, R1W; Coconino; 6,428 feet; 224.10;
    a. 1.8 acres; 1970; cattle, deer; juniper cleared.

262. Three Lakes Study Plot: SE1/4 sec. 6, T37N, R2E; Coconino; 8,300 feet; 421.00;
    a. 660 by 396 feet; 1959; vegetation data on file; cattle; rototilled and planted to grass.

263. VT Exclosure: SW1/4 sec. 12, T35N, R2E; Coconino; 8,747 feet; 411.00;
    a. 5 acres; 1953; vegetation data on file; photos on file; cattle, deer; enlarged in 1962.
    b. 5 acres; 1962; vegetation data on file; photos on file; cattle.

264. White Pockets - Eastslide: SE1/4 sec. 6, T37N, R1W; Coconino; 6,300 feet; 224.10;
    a. 80 acres; 1954; vegetation data on file; photos on file; cattle; juniper cleared one-half acre; grass seeded one-half cleared area.

265. White Pockets Study Plot: NW1/4 sec. 9, T37N, R2W; Coconino; 6,100 feet; 224.10;
    a. 3.75 acres; 1960; vegetation data on file; cattle.
    b. 0.5 acre; 1960; vegetation data on file; cattle, deer; small plot enclosed in large plot.

Tusayan Ranger District

266. Hull Tank Administrative Site: Sec. 22, T30N, R4E: Coconino; 6,600 feet; 221.20;
    a. 480 acres; 1907; livestock.

267. McRae Study Plot: NW1/4 sec. 2, T29N, R4E; Coconino; 7,200 feet; 422.10;
    a. 30 by 30 feet; livestock; establishment date unknown.

268. Skinner Ridge Study Plots: SE1/4 sec. 18, T29N, R4E; Coconino; 7,200 feet; 221.20;
    a. 1 acre approx.; vegetation data on file; cattle, deer.
    b. 1 acre approx.; vegetation data on file; cattle; establishment date for both plots unknown.

269. Willows Camp Exclosure: NE1/4 sec. 13, T28N, R6E; Coconino; 6,600 feet; 422.10;
    a. 300 by 300 feet approx.; 1964; livestock; established between 1963 and 1965.

Williams Ranger District

270. AA Plot No. 1: NE1/4 sec. 4, T23N, R1W; Coconino; 5,800 feet; 422.10;
    a. 0.1 acre; 1932; vegetation data on file; sheep; recent juniper establishment.

271. Devil Dog Summer-Rim Plot No. 3: NW1/4 sec. 8, T21N, R1E; Coconino; 6,500 feet; 224.10;
    a. 0.1 acre; 1939; vegetation data on file; photos on file; cattle; area outside exclosure cabled in early 1950's.

272. Devil Dog Winter Plot No. 5: SW1/4 sec. 32, T21N, R1W; Coconino; 5,400 feet; 224.10;
    a. 0.1 acre; 1939; vegetation data on file; photos on file; cattle; area outside exclosure cabled in early 1950's.

273. Indian Mesa Remote Area: NW1/4 sec. 23, T21N, R1W; Coconino; 5,980 feet; 422.10;
    a. 10 acres; vegetation data on file; photos on file; livestock.

274. Irishman Dam Plot No. 4; SE1/4 sec. 31; T21N, R1W; Coconino; 5,200 feet; 224.10;
    a. 0.1 acre; 1939; vegetation data on file; photos on file; cattle, sheep; juniper becoming established.

275. Old Biological Survey Plot No. 2: NW 1/4 sec. 3, T22N, R2E; Coconino; 6,400 feet; 224.10;
    a. 0.35 acres; 1918; vegetation data on file; photos on file; cattle.
    b. 0.43 acres; 1918; vegetation data on file; photos on file; cattle, rodents; first two plots rebuilt in 1939.
    c. 0.1 acre; 1918; vegetation data on file; photos on file; cattle, rodents; (Clements et al. 1927, Clements et al. 1930, Clements et al. 1932, Taylor and Loftfield 1922, Taylor and Loftfield 1924).

276. Pingue Plot No. 1: NE1/4 sec. 10, T22N, R2E; Coconino; 6,400 feet; 224.10;
    a. 0.5 acre; 1939; vegetation data on file; photos on file; cattle.

277. Relict Mesa-Tule Allotment: NW1/4 sec. 16, T20N, R3E; Coconino; 6,900 feet; 221.20;
    a. 1-2 acres; vegetation data on file; photos on file; livestock; remote area.

278. Thirteen Mile Tank Plot No. 6: NE 1/4 sec. 10, T21N, R1W; Coconino; 5,800 feet; 224.10;
    a. 0.1 acre; 1939; vegetation data on file; photos on file; cattle; area outside exclosure cabled in early 1950's.

Prescott National Forest

Chino Valley Ranger District

279. Bar Heart Plot: NW1/4 sec. 26, T19N, R1W; Yavapai; 4,600 feet; 422.10;
    a. 1 acre; 1940; photos on file; livestock.

280. Paulden Exclosure (AGF): SE1/4 sec. 23, T18N, R2W; Yavapai; 4,700 feet; 224.10;
    a. 1 acre; 1958; cattle, deer.

281. Witty Tom Plot 1: NW1/4 sec. 12, T18N, R1E; Yavapai; 4,632 feet; 422.10;
    a. 200 by 200 feet; 1962; vegetation data on file; photos on file; cattle, horses.

282. Witty Tom Plot 2: NW1/4 sec. 12, T18N, R1E; Yavapai; 4,632 feet; 422.10;
    a. 200 by 200 feet; 1962; vegetation data on file; photos on file; cattle, horses; one-fourth mile from Witty Tom Plot 1.

Crown King Ranger District

283. Lane Mountain Watershed: T9N, R1W; Yavapai; 3,400-6,700 feet; 221.00, 223.00, 323.00, 423.00, 531.10; 25,000 acres; 1975; livestock; also in T9-1/2N, T10N, R1E.

284. Lassard Study Plot: SE1/4 sec. 33, T12N, R1E; Yavapai; 3,500 feet; 423.60;
    a. 66 by 66 feet; 1925; vegetation data on file; photos on file; cattle, horses.

285. Rabbit Springs Riparian Exclosure: NW1/4 sec. 21, T10N, R2W; Yavapai; 3,400 feet; 223.20;
    a. 4.5 acres; 1977; photos on file; cattle, horses.

Thumb Butte Ranger District

286. Buckman Flats (AGF): NE1/4 sec. 7, T14N, R3W; Yavapai; 5,400 feet; 323.10;
    a. 1 acre; 1939; cattle.
    b. 1 acre; 1939; cattle, deer; converted to deer-cattle exclosure in 1958 by AGF.

287. Doce Siding (AGF): NW1/4 sec. 17, T14N, R3W; Yavapai; 5,600 feet; 323.10;
    a. 1 acre; 1956; cattle.
    b. 1 acre; 1956; cattle, deer.

Verde Ranger District

288. Beasley Flat Wildlife Exclosure: Sec. 26, 34, 35, T13N, R5E; Yavapai; 3,100 feet; 423.60;
    a. 130 acres; 1976; vegetation data on file; photos on file; cattle; root plowed, disced, grass seeded.

289. Johnson Wash Research Area: W1/2 sec. 4, E1/2 sec. 5, T13N, R3E; Yavapai; 4,700 feet; 323.10;
    a. 90 acres; 1965; vegetation data on file; cattle.

290. Lucky Canyon Erosion Plot: NW1/4 sec. 12, T13N, R4E; Yavapai; 3,000 feet; 423.50;
    a. 150 acres; 1965; photos on file; cattle.

291. Sycamore Wildlife Exclosure: Sec. 16, 20, 21, T11N, R5E; Yavapai; 5,200 feet; 223.10;
    a. 1 mile by 150 feet; 1972; photos on file; cattle.

292. Yellow Jacket Wildlife Exclosure: NE1/4 sec. 33, T12N, R3E; Yavapai; 3,750 feet; 223.20;
    a. 1/4 mile by 300 feet; 1975; cattle.

Walnut Creek Ranger District

293. Brushy Mt. Wildlife Exclosure: NW1/4 sec. 2, T16N, R6W; Yavapai; 5,800 feet; 221.20;
    a. 1 acre; 1974; vegetation data on file; photos on file; cattle; seeded to grass following brush crushing.

294. Camp Wood Study Plot: NW1/4 sec. 3, T16N, R6W; Yavapai; 5,800 feet; 221.20;
    a. 1 acre; 1939; vegetation data on file; photos on file; cattle.

295. Hyde Creek Riparian Study Exclosure: SW1/4 sec. 18, T17N, R5W; Yavapai; 5,500 feet; 223.10;
    a. 10 acres; 1974; vegetation data on file; photos on file; cattle.

296. Juniper Control Study Plot: SW1/4 sec. 4, T18N, R5W; Yavapai; 5,000 feet; 423.60;
    a. 1 acre; 1949; vegetation data on file; cattle; juniper removed; seeded to grass.

297. Parker Springs Study Plot: NW1/4 sec. 19, T17N, R5W; Yavapai; 5,500 feet; 323.10;
    a. 1 acre; 1939; vegetation data on file; photos on file; cattle; not checked since 1964.

298. Pine Creek Riparian Study Exclosure: NW1/4 sec. 25, T17N, R6W; Yavapai; 5,500 feet; 223.10;
    a. 10 acres; 1975; vegetation data on file; photos on file; cattle.

299. Red Mountain Study Plot: NE1/4 sec. 18, T19N, R5W; Yavapai; 5,000 feet; 422.10;
    a. 1 acre; 1939; vegetation data on file; photos on file; cattle; exclosure not checked recently.

300. Smith Mesa Study Plot: SW1/4 sec. 30, T16N, R5W; Yavapai; 5,000 feet; 423.60;
    a. 2 acres; 1963; vegetation data on file; photos on file; cattle; seeded to grass in 1966.

301. South Fork Exclosure (AGF): W1/2 sec. 30, T18N, R6W; Yavapai; 5,600 feet; 224.10;
    a. 1 acre; 1965; cattle.

302. Warren Exclosure: SW1/4 sec. 32, T18N, R6W; Yavapai; 5,900 feet; 224.10;
    a. 1 acre; 1965; cattle.

Tonto National Forest

Cave Creek Ranger District

303. Blackjack Plot: Sec. 18, T8N, R5E; Yavapai; 4,400 feet; 323.10;
    a. 2 acres; 1939; vegetation data on file; photos on file; cattle.

304. Bronco-St. Clair Study Plot: NW1/4 sec. 22, T6N, R5E; Maricopa; 2,200 feet; 531.10;
  a. 2.5 acres; 1940; vegetation data on file; photos on file; cattle, sheep.
  b. 2.5 acres; 1940; vegetation data on file; photos on file; cattle, sheep.

305. Camp Creek Divide: Sec. 26, T7N, R5E; Maricopa; 3,500 feet; 323.10;
  a. 4 acres; 1924; vegetation data on file; photos on file; cattle; plot enlarged in 1940.

306. Magazine Mesa: Sec. 30, T8N, R5E; Maricopa; 4,000 feet; 422.10;
  a. 30 acres; 1940; vegetation data on file; photos on file; cattle.

Globe Ranger District

307. Boyce Thompson Southwest Arboretum: Sec. 33, T2S, R12E; Pinal; 2,400-3,000 feet; 223.20, 423.60;
  a. 725 acres; 1924; vegetation data on file; photos on file; cattle; also in R11E; jointly managed by ASPB, BTSA, and UA.

308. Capitan Exclosure: NE1/4 sec. 14, T2S, R15E; Gila; 5,000 feet; 323.10;
  a. 150 by 150 feet; photos on file; cattle; grazed briefly in 1978; establishment date unknown.

309. Chrysotile Demonstration Plot: SE1/4 sec. 21, T4N, R17E; Gila; 5,800 feet; 422.10;
  a. 5 acres; 1945; photos on file; cattle.

310. Fritz Special Use Pasture: NW1/4 sec. 13, T1S, R15E; Gila; 3,600 feet; 423.10;
  a. 60 acres; 1961; photos on file; cattle.

311. Jones Water: NE1/4 sec. 23, T3N, R16E; Gila; 4,287 feet; 423.10;
  a. 1/2 by 1/4 mile; photos on file; cattle; establishment date unknown.

312. JU Pasture Exclosure: NE1/4 sec. 15, T4N, R16E; Gila; 4,500 feet; 323.10;
  a. 240 square feet; photos on file; cattle; establishment date unknown; rebuilt in 1978.

313. Murry Hill Sample Plot: NE1/4 sec. 4, T2N, R14E; Gila; 4,000 feet; 423.10;
  a. 100 by 200 feet; photos on file; cattle; seeded to weeping lovegrass.

314. Nugget Mesa Rd.-Radium Allotment: SE1/4 sec. 22, T2N, R15E; Gila; 3,700 feet; 423.10;
  a. 50 by 50 feet; photos on file; cattle, horses; establishment date unknown.
  b. 132 by 132 feet; 1978; photos on file; cattle, horses; new fence includes previous exclosure.

315. Ray Road Exclosure: NW1/4 sec. 36, T2S, R12E; Pinal; 3,200 feet; 423.10;
  a. 1,200 by 450 feet; 1935; vegetation data on file; photos on file; cattle; establishment date approximate.

316. Sedow Allotment: SW1/4 sec. 3; T3N, R16E; Gila; 4,200 feet; 423.10;
  a. 200 by 200 feet; photos on file; cattle; establishment date unknown.

317. Storm Canyon Pasture Exclosure: NE1/4 sec. 6, T3N, R16E; Gila; 4,000 feet; 323.10;
  a. 50 by 50 feet; photos on file; cattle; establishment date unknown.

318. Summit plots: Sec. 4, T2N, R14E; Gila; 3,600 feet; 323.10, 531.10;
  a. 0.37 acre; 1925; vegetation data on file; photos on file; cattle.
  b. 1.23 acres; 1925; vegetation data on file; photos on file; cattle.
  c. 0.59 acre; 1925; vegetation data on file; photos on file; cattle.
  d. 0.49 acre; 1925; vegetation data on file; photos on file; cattle; shrub control and reseeding in first four plots.
  e. 0.43 acre; 1925; vegetation data on file; photos on file; cattle.
  f. 1.05 acres; 1925; vegetation data on file; photos on file; cattle.
  g. 0.49 acre; 1925; vegetation data on file; photos on file; cattle.
  h. 0.80 acre; 1925; vegetation data on file; photos on file; unfenced check plot.
  i. 0.54 acre; 1925; vegetation data on file; photos on file; unfenced check plot.

319. Winters Ranch Plot No. 79: SW1/4 sec. 32, T3N, R16E; Gila; 4,800 feet; 423.10;
  a. 200 by 200 feet; 1939; cattle; enlarged in 1944.

Mesa Ranger District

320. Blue Point Study Plot: Sec. 15, T2N, R7E; Maricopa; 1,800 feet; 531.10;
  a. 1 acre approx.; cattle, sheep; establishment date unknown.

321. Brushy Basin Exclosure: NE1/4 sec. 3, T4N, R9E; Maricopa; 4,000 feet; 323.10;
  a. 10 acres; 1969; cattle, deer; plot burned and seeded to Lehmann lovegrass.

322. Cross F Study Plot: NW1/4 sec. 19, T7N, R9E; Maricopa; 4,000 feet; 422.10;
  a. 12 acres; 1934; vegetation data on file; photos on file; cattle.

Payson Ranger District

323. Buckhead Mesa Exclosure: NW1/4 sec. 3, T11N, R9E; Gila; 5,200 feet; 224.10;
    a. 93 acres; 1935; photos on file; cattle.

324. Control Rd. Exclosure: SW1/4 sec. 36, T11N, R11E; Gila; 5,800 feet; 224.10;
    a. 60 acres approx.; cattle; establishment date unknown.

325. Deadman Mesa: SE1/4 sec. 24, T12N, R7E; Gila; 5,900 feet; 224.10;
    a. 60 acres; vegetation data on file; photos on file; cattle; established before 1942.

326. Houston Mesa Enclosure: SE1/4 sec. 13, T11N, R10E; Gila; 5,000 feet; 224.10;
    a. 4 acres; cattle; appears to have had junipers pushed; establishment date unknown.

Pleasant Valley Ranger District

327. Aztec "B" Wildlife Plot: SE1/4 sec. 24, T6N, R13E; Gila; 7,000 feet; 221.20, 223.00;
    a. 10 acres; 1964; cattle; includes NW1/4 Sec.24.

328. Bottle Springs: SE1/4 sec. 6, T9N, R14E; Gila; 7,000 feet; 221.20;
    a. 4 acres approx.; 1962; cattle.

329. McInturf Springs: NW1/4 sec. 27, T10N, R14E; Gila; 5,400 feet; 225.20;
    a. 10 acres; 1960; cattle, sheep; establishment date approx.; seeded to weeping lovegrass.

330. Pine Creek Range Study Plot: N1/2 sec. 36, T10N, R13E; Gila; 5,900 feet; 422.00;
    a. 70 acres; 1940; vegetation data on file; photos on file; cattle, sheep; original small plot enlarged unknown date; some cattle use.

331. Pine Springs Wildlife Area: Sec. 29, 30, T10N, R15E; Gila; 5,500 feet; 224.10;
    a. 110 acres approx.; 1942; vegetation data on file; cattle; grazed 1977; seeded 1973, wheatgrass, clover.

332. Pleasant Valley Station Exclosure: NW1/4 sec. 29, T9N, R14E; Gila; 5,000 feet; 224.10;
    a. 0.3 acre; 1941; vegetation data on file; photos on file; horses.

333. Red Lake: Sec. 27, T10N, R15E; Gila; 6,500 feet; 221.20;
    a. Size unknown; 1940; vegetation data on file; photos on file; cattle; seeded; refenced in 1973.

334. Red Lake Study Plots: SW1/4 sec. 27, T10N, R14E; Gila; 6,500 feet; 221.20;
    a. 5 acres; 1934; vegetation data on file; photos on file; cattle; cattle occasionally grazed until 1974 when fence repaired.

335. SAEF Workman Creek Watersheds: Sec. 33, T6N, R14E; Gila; 6,500 feet; 221.10, 221.20;
    a. 1,087 acres; 1938; vegetation data on file; photos on file; cattle.

336. Thurlo: SE1/4 sec. 9, T9N, R13E; Gila; 5,300 feet; 224.10;
    a. 80 acres approx.; 1966; cattle; seeded to several grass species.

337. Zellner-Cline: SE1/4 sec. 2, T9N, R14E; Gila; 6,500 feet; 221.20;
    a. 5 acres approx.; 1964; cattle; Seeded with weeping lovegrass and orchard grass in 1965.

Roosevelt Ranger District

338. Three Bar Wildlife Area: T4N, R11E; Gila; 2,900-7,691 feet; 221.00, 223.00, 224.00, 225.00, 233.00, 323.00, 424.00, 531.00;
    a. 38,897 acres; 1947; cattle; Also in T4N, R10E; T3N, R10E and R11E. (27).

Tonto Basin Ranger District

339. Black Hills: Sec. 34, T4N, R13E; Gila; 2,225 feet; 531.10;
    a. 190 acres; 1937; vegetation data on file; photos on file; cattle; Both plots also in sec. 3 T3N.
    b. 75 acres; 1958; vegetation data on file; photos on file; cattle; small plot seeded in 1958; grazed intermittently.

340. Deer Creek Plot: Sec. 7, T8N, R10E; Gila; 3,275 feet; 423.10;
    a. 40 acres; 1940; vegetation data on file; photos on file; cattle; seeded to Lehmann lovegrass, 1960.
    b. 40 acres; 1960; vegetation data on file; photos on file; cattle; both plots grazed from 1968 until fence repaired in 1978.

341. Dutchwoman Butte Remote Area: Sec. 14, T5N, R12E; Gila; 5,000 feet; 422.10;
    a. 0.15 square mile; vegetation data on file; livestock; frequent natural burning.

342. Horrell Study Plot: SW1/4 sec. 9, T3N, R13E; Gila; 2,400 feet; 531.10;
    a. 50 acres; 1937; vegetation data on file; photos on file; cattle; rebuilt in 1962.

343. SAEF Natural Drainages: NW1/4 sec. 13, T5N, R13E; Gila; 4,600 feet; 323.10;
   a. 54 acres; 1936; vegetation data on file; photos on file; cattle.

NATIONAL PARK SERVICE

Canyon de Chelly

344. Wide Rock Butte Remote Area: T5N, R9W; Apache; 6,800 feet; 224.10;
   a. 30 acres; deer, livestock; (Schmutz et al. 1967).

Casa Grande National Monument

345. Casa Grande Ruins National Monument: Sec. 16, T5S, R8E; Pinal; 1,420 feet; 531.20;
   a. 482 acres; 1930; livestock; (Judd et al. 1971).

Chiricahua National Monument

346. Chiricahua National Monument: T16S, R29E; Cochise; 5,000-6,000 feet; 222.00, 225.00;
   a. 11,000 acres; 1924; livestock; approximately 600 acres grazed until 1974; also in T17S, R30E.

Glen Canyon National Recreation Area

347. Antelope Island: T41N, R9E; Coconino; 4,200 feet; 521.30;
   a. 10,000 acres; 1977; livestock; island formed by Lake Powell.

Grand Canyon National Park

348. Boysag Point Remote Area: Sec. 8, T34N, R4W; Mohave; 5,500 feet; 224.10, 521.10;
   a. 70 acres; vegetation data on file; livestock; (Schmutz et al. 1967).

349. Desert View Exclosure: SE1/4 sec. 5, T30N, R5E; Coconino; 7,250 feet; 224.10;
   a. 34 by 74 feet; 1934; vegetation data on file; cattle.

350. Fishtail Mesa Remote Area: Coconino; 6,000-6,200 feet; 224.00, 521.00;
   a. 1,430 acres; vegetation data on file; photos on file; livestock; Latitude 36° 26′ N, Longitude 112° 34′ W; (Jameson et al. 1962).

351. Grand Canyon National Park: Coconino; 960-9,125 feet; 211.00, 212.00, 221.00, 223.00, 224.00, 233.00, 411.00, 421.00, 521.00, 522.00;
   a. 900,000 acres; 1919; vegetation data on file; photos on file; livestock; enlarged most recently in 1975; some burro use; an additional 294,000 acres grazed by livestock; (McDougall 1947).

352. Grandview: SE1/4 sec. 21, T30N, R4E; Coconino; 7,480 feet; 221.20;
   a. 50 by 58 feet; 1934; vegetation data on file; cattle.

353. Lipan Point Exclosure: SE1/4 sec. 33, T31N, R5E; Coconino; 7,250 feet; 224.10;
   a. 41 by 49 feet; 1934; cattle.

354. Quarry Road Exclosure: SE1/4 sec. 14, T30N, R4E; Coconino; 7,000 feet; 224.10;
   a. 50 by 50 feet; 1934; vegetation data on file; cattle.

355. South Entrance Experimental Plot No. 8: NE1/4 sec. 25, T31N, R2E; Coconino; 6,940 feet; 221.20;
   a. 80 by 40 feet; 1935; vegetation data on file; cattle, deer, rabbits.

356. Ten X Road: SE1/4 sec. 18, T30N, R4E; Coconino; 7,400 feet; 221.20;
   a. 58 by 66 feet; 1934; vegetation data on file; deer.

357. Yaki Burn: Sec. 19, T31N, R3E; Coconino; 7,200 feet; 224.10;
   a. 29 by 39 feet; 1956; vegetation data on file; deer; used to study postfire recovery without deer access.

Montezuma Castle National Monument

358. Montezuma Castle: Sec. 8, 16, 17, T14N, R5E; Yavapai; 3,300 feet; 423.00, 531.10;
   a. 500 acres; 1959; livestock; riparian area grazed; (McDougall 1960).

359. Montezuma Well: Sec. 31, T15N, R6E; Yavapai; 3,600 feet; 423.00, 531.10;
   a. 240 acres; 1959; livestock; partly in sec. 6, R5E; (Spangle and Sutton 1949).

Navajo National Monument

360. Betatakin Ruin: Navajo; 6550-7150 feet; 224.10;
   a. 240 acres; 1967; vegetation data on file; livestock; Latitude 36° 41′ N, Longitude 110°32′ W.

361. Keet Seel Ruin: Navajo; 6,750-7,550 feet; 224.10;
   a. 160 acres; 1967; vegetation data on file; livestock; Latitude 36° 46′ N, Longitude 110° 30′ W.

Organ Pipe National Monument

362. Armenta Well Exclosure: N1/2 sec. 24, T14S, R6W; Pima; 1,570 feet; 531.20;
   a. 9.9 acres; 1963; vegetation data on file; photos on file; livestock.

363. Dos Lomitas Exclosure: NW1/4 sec. 14, T18S, R5W; Pima; 1,375 feet; 531.70;
  a. 3.2 acres; 1963; vegetation data on file; photos on file; livestock.

364. Organ Pipe Cactus National Monument: Pima; 1,000-4,408 feet; 423.00, 531.10, 531.20, 531.70;
  a. 330,779 acres; 1937; vegetation data on file; photos on file; livestock; all cattle removed in 1978.

Petrified Forest National Monument

365. Petrified Forest National Monument: Apache and Navajo; 5,300-6,235 feet; 224.10, 422.00, 521.00;
  a. 93,492 acres; 1935; livestock; completely fenced in 1968.

Saguaro National Monument

366. Rincon Mountain Unit: Pima; 2,700-8,660 feet; 221.00, 222.00, 223.00, 225.00, 233.00, 421.00, 423.00, 531.00;
  a. 62,332 acres; 1933; livestock; grazing phased out 1958- 1978; equestrian use in some areas.

367. Rodent-Proof Exclosure No. 1: NW1/4 sec. 20, T14S, R16E; Pima; 2,960 feet; 531.10;
  a. 50 by 50 feet; 1962; vegetation data on file; photos on file; livestock, rodents; surrounding area ungrazed by cattle since 1958.

368. Rodent-Proof Exclosure No. 2: NE1/4 sec. 20, T14S, R16E; Pima; 2,970 feet; 531.10;
  a. 50 by 50 feet; 1962; vegetation data on file; photos on file; livestock, rodents; surrounding area ungrazed by cattle since 1958.

369. Rodent-Proof Exclosure No. 3: NE1/4 sec. 28, T14S, R16E; Pima; 3,200 feet; 531.10;
  a. 50 by 50 feet; 1962; vegetation data on file; photos on file; livestock, rodents; surrounding area ungrazed by cattle since 1958.

370. Tucson Mountain Unit: Pima; 2,178-4,687 feet; 423.00, 531.00;
  a. 16,669 acres; 1929; vegetation data on file; photos on file; livestock.

Tonto National Monument

371. Tonto National Monument: Sec. 26, 27, 34, 35, T4N, R12E; Gila; 2,300-4,000 feet; 323.00, 531.00;
  a. 652 acres; 1941; livestock.
  b. 468 acres; 1978; livestock; (Burgess 1965).

Tuzigoot National Monument

372. Tuzigoot National Monument: W1/2 sec. 22, T16N, R3E; Yavapai; 3,450 feet; 423.00, 531.10;
  a. 43 acres; 1959; livestock.

Walnut Canyon National Monument

373. Walnut Canyon Island Remote Area: SE1/4 sec. 26, T21N, R8E; Coconino; 6,700 feet; 221.10; 221.20, 223.10, 224.10, 521.10;
  a. 130 acres; photos on file; livestock; (Smith 1974).

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374. Page-Trowbridge Experimental Ranch: S1/2 sec. 27, N1/2 sec. 34, T9S, R14E; Pinal; 3,700 feet; 423.10;
  a. 640 acres; 1941; vegetation data on file; photos on file; cattle; (Smith and Schmutz 1975).

ADDENDUM

The following reference areas were reported too late to be included in the main listing of this report:

BUREAU OF LAND MANAGEMENT

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375. Clayhole Exclosure, Middle: SE1/4 sec. 20, T39N, R7W; Mohave; 4,900 feet; 521.20;
  a. 330 by 330 feet; 1951; vegetation data on file; photos on file; livestock.

376. Clayhole Exclosure, North: NW1/4 sec. 10, T40N, R7W; Mohave; 4,980 feet; 422.00;
  a. 330 by 330 feet; 1951; vegetation data on file; photos on file; livestock.

377. Clayhole Exclosure, South: NW1/4 sec. 29, T38N, R7W; Mohave; 4,965 feet; 422.00;
  a. 330 by 330 feet; 1951; vegetation data on file; photos on file; livestock.

378. Spy Mesa Remote Area: NW1/4 sec. 25, T41N, R8W; Mohave; 5,000 feet; 224.10;
  a. 40 acres; vegetation data on file; photos on file; livestock; (Thatcher and Hart 1974).

FOREST SERVICE

Coronado National Forest

Nogales Ranger District

379. Bog Hole Waterfall Area (AGF): NW1/4 sec. 32, T22S, R17E; Santa Cruz; 5,075 feet; 223.20, 422.00;
   a. 50 acres; 1978; livestock.

MULTIPLE OWNERSHIP

Arizona State Land Department, Bureau of Land Management, and Private

380. Wickenburg Inn: Sec. 7, 8, 9, 10, 15, 16, 17, 18, 20, 21, T8N, R5W; Yavapai; 2,200 by 2,750 feet; 531.10;
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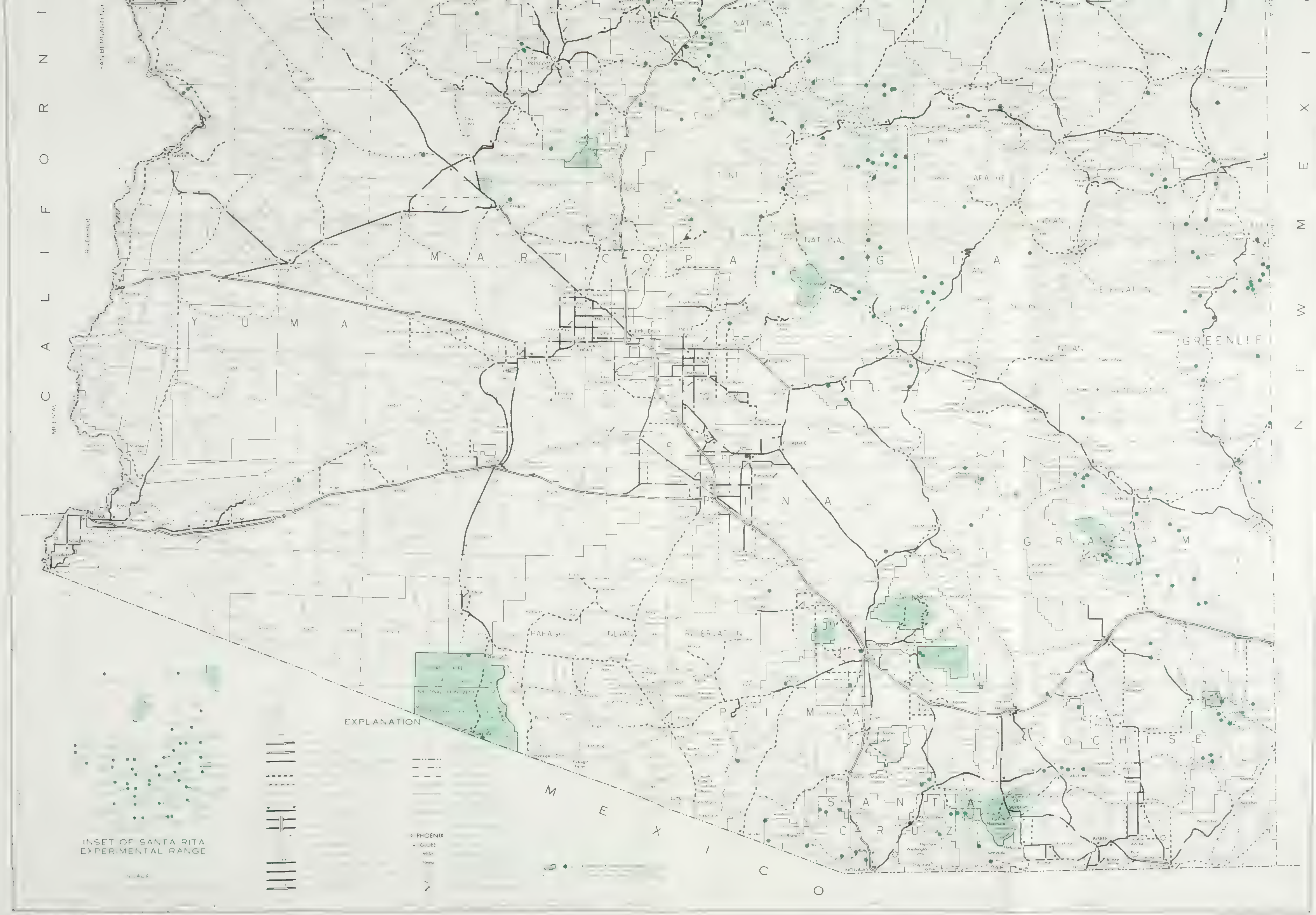

BASE PREPARED BY ARIZONA DEPARTMENT OF TRANSPORTATION PHOTOGRAMMETRY AND MAPPING SERVICES IN COOPERATION WITH UNITED STATES DEPARTMENT OF TRANSPORTATION FEDERAL HIGHWAY ADMINISTRATION

MAP OF ARIZONA SHOWING RANGE REFERENCE AREAS

COMPILED BY R. M. TURNER AND L. H. APPLEGATE, U.S. GEOLOGICAL SURVEY,
P. M. BERGTHOLD, ARIZONA STATE PARKS;
S. GALLIZIOLI, ARIZONA STATE GAME AND FISH DEPARTMENT;
AND S. C. MARTIN, U.S. FOREST SERVICE

1980

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General Technical Report RM-79
Rocky Mountain Forest and
Range Experiment Station
Forest Service
U.S. Department of Agriculture

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

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Lincoln, Nebraska
Lubbock, Texas
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A Bibliography of the Lesser Prairie Chicken, 1873-1980.

John A. Crawford and Fred A. Stormer

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Rocky Mountain Forest and
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USDA Forest Service
General Technical Report RM-80

November 198

A Bibliography of the Lesser Prairie Chicken, 1873-1980

John A. Crawford, Associate Professor
Oregon State University
and
Fred A. Stormer, USDA Forest Service
Rocky Mountain Forest and Range Experiment Station[1]

Abstract

This bibliography contains 207 references on research and management of the lesser prairie chicken (*Tympanuchus pallidicinctus)* published during 1873-1980. A subject index is referenced numerically to an alphabetical list of authors.

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[1] *Headquarters is at Fort Collins in cooperation with Colorado State University. Research reported here was completed at the Station's Research Work Unit in Lubbock, Tex.*

A Bibliography of the Lesser Prairie Chicken, 1873-1980

John A. Crawford and Fred A. Stormer

Lesser prairie chickens (*Tympanuchus pallidicinctus*) once occupied large areas of grasslands in southeastern Colorado, southwestern Kansas, eastern New Mexico, western Oklahoma, and the Texas Panhandle. Since 1900, the occupied range has declined by 92% (Taylor and Guthery 1980). Intensive agriculture and heavy grazing probably was a major factor in reducing populations. The species is not endangered; however, land use practices associated with its decline continue, and in some portions of the range, are expanding as more rangeland is converted to irrigated cropland. Hence, the situation bears close watching by conservationists and land managers alike, especially in light of the fact that only about 5% of the currently occupied range is in public ownership.

Because of the large amount of wildlife literature that has accumulated, it is difficult for biologists to cope with the volume of information, even on a regional basis. This bibliography may help them by providing sources of information on the lesser prairie chicken.

More than 200 documents (books, technical and popular articles, theses, dissertations, and reports) relating to the lesser prairie chicken have been published since the identification of this species in 1873. Approximately 75% of these works have been published since 1950. Of the 207 references listed in this bibliography, 60% deal specifically with the lesser prairie chicken; the remainder are general references in which the species is included.

Many Federal Aid in Wildlife Restoration Project reports were included because much of the information in these reports is not published elsewhere. The reports are available from the Fish and Wildlife Reference Service, Denver Public Library, Denver, CO 80223.

This bibliography is divided into two parts, a subject index and an author index. There are nineteen categories in the subject index with numbers which relate to works listed in the alphabetical author index.

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Rocky Mountains

Southwest

Great Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

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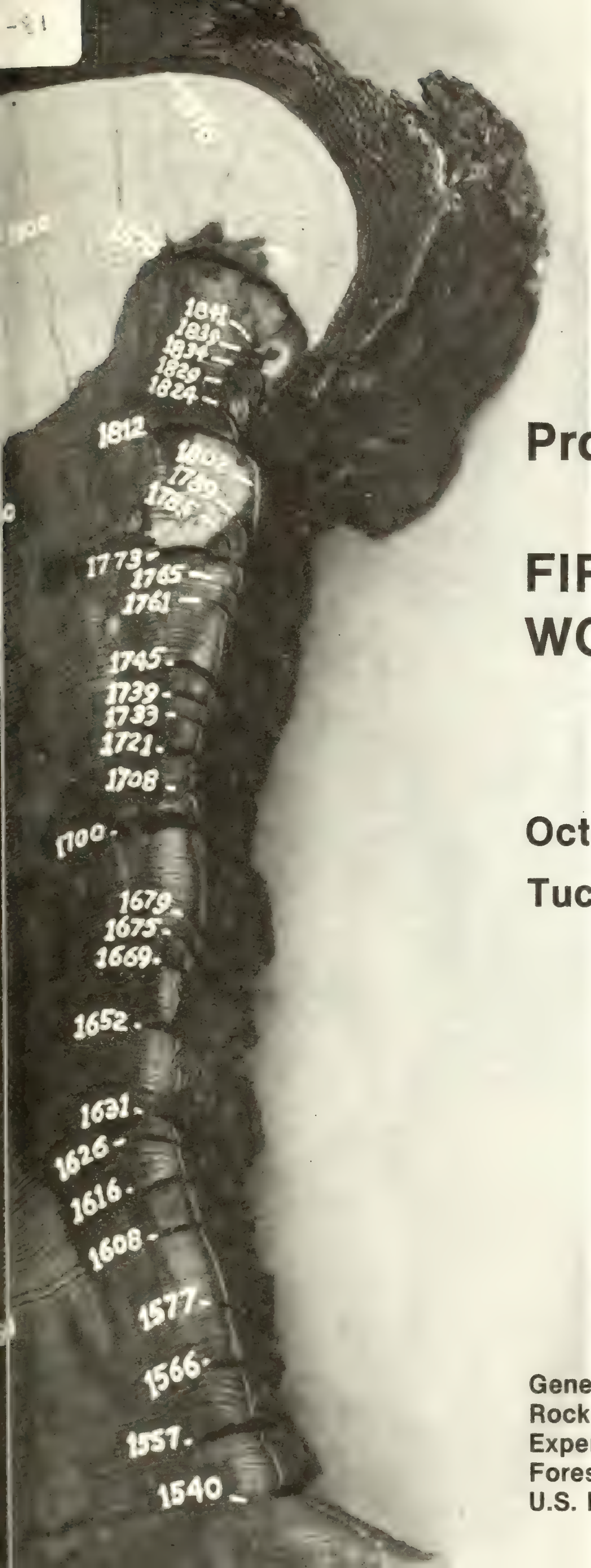

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Proceedings of the

FIRE HISTORY WORKSHOP

October 20-24, 1980
Tucson, Arizona

General Technical Report RM-81
Rocky Mountain Forest and Range
Experiment Station
Forest Service
U.S. Department of Agriculture

Dedication

The attendees of The Fire History Workshop wish to dedicate these proceedings to Mr. Harold Weaver in recognition of his early work in applying the science of dendrochronology in the determination of forest fire histories; for his pioneering leadership in the use of prescribed fire in ponderosa pine management; and for his continued interest in the effects of fire on various ecosystems.

Stokes, Marvin A., and John H. Dieterich, tech. coord. 1980. Proceedings of the fire history workshop. October 20-24, 1980, Tucson, Arizona. USDA Forest Service General Technical Report RM-81, 142 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

The purpose of the workshop was to exchange information on sampling procedures, research methodologies, preparation and interpretation of specimen material, terminology, and the application and significance of findings, emphasizing the relationship of dendrochronology procedures to fire history interpretations.

Proceedings of the FIRE HISTORY WORKSHOP

October 20-24, 1980
Tucson, Arizona

Marvin A. Stokes and John H. Dieterich
Technical Coordinators

Sponsored By:

Rocky Mountain Forest and Range Experiment Station
Forest Service, U.S. Department of Agriculture

and

Laboratory of Tree-Ring Research
University of Arizona

General Technical Report RM-81
Rocky Mountain Forest and Range
Experiment Station

Forest Service
U.S. Department of Agriculture
Fort Collins, Colorado

Foreword

Fire has played a role in shaping many of the plant communities found in the world today. Just how important this role has been can only be determined after we know more about the frequency, extent, and intensity of these historical fires. The Fire History Workshop, first of its kind held anywhere in the world, held as its primary objective the exchange of information on techniques and methodologies for determining fire histories based on tree-ring evidence. In addition, the workshop provided a forum for reporting on current, or recently completed fire history studies; made facilities and expertise available through the Laboratory of Tree-Ring Research for inspecting fire-scarred specimens and answering specific questions concerning dating and interpretation of the fire-scarred material; and helped resolve problems in terminologies which so frequently accompany developing sciences.

The study of fire scars as reflected in the radial growth patterns of both softwoods and hardwood tree species provides an important means of securing information on the precise years in which fires occurred during centuries past. The fire-scarred material collected and studied represents a form of "natural resource artifact"--much as the pot-sherd or spear point represent cultural artifacts of past civilization. These natural resource artifacts are disappearing and one day will be totally absent from forested areas due to the influence of logging, fire, natural mortality and deterioration. Even the material holding historical fire evidence currently being protected in National Parks, Natural Areas, and other reserves will eventually be returned to the soil through natural processes. For this reason, it seems imperative that those collecting fire-scarred material for study insure that representative specimens are properly described, cataloged, preserved, and protected so that they will be available for future studies if needed.

Since the early 1970's there has been a renewed interest in the use of tree rings and fire scars as a means of describing historical fires. Both living and dead material have been represented. This renewed interest has been generated in part by the general recognition that fire effects are not always destructive, and that in fact there are many beneficial aspects of fire when it burns under prescribed conditions of fuel, weather, and topography. The increased awareness of the need to return fire to its natural role in various ecosystems has also prompted this renewed interest for without knowing what the natural fire cycles have been in the past, it will be impossible to realistically reintroduce fire into these same ecosystems.

The Laboratory of Tree-Ring Research played an extremely important role in this workshop. If the science of dendrochronology is to be used in the process of identifying and describing the incidence of historical fires, the established guidelines and procedures for analyzing the material and expressing the results should be carefully adhered to! Personnel at the Laboratory of Tree-Ring Research willingly provided this assistance and thos attending the workshop benefited directly from this store of knowledge and experience.

There was a consensus that a similar forum be held in the future to provide an opportunity to report on completed studies and propose new work relating to dendrochronology and fire history. Our workshop provided only limited opportunity for reporting on fire effects and plant succession and on paleoecological studies. We anticipate that this will not change much in the immediate future because of the need to continue to resolve problems in utilizing dendrochronological techniques in determining fire histories; and the fact that ample opportunitie will be available through other outlets to report on immediate and long-term effects of single and multiple burns. Additional subjects that might be covered in a future workshop include the mechanics of fire-scarring and physiology of the recovery process, statistical sampling problems related to fire history studies, and application of fire history studies in management situations.

Workshop proceedings are notoriously late in reaching the hands of workshop attendees and ultimat users of the information. To speed up publication of these proceedings Robert Hamre, Editor, Rocky Mountain Forest and Range Experiment Station, contacted each author asking them to assume full responsibility for submitting manuscripts in camera-ready format by the time the workshop convened. Bob was largely successful in this effort and we appreciate his efforts in getting the proceedings processed and published.

Many individuals assisted in making the worksho a success. Dr. Bryant Bannister, Director, and members of his staff at the Laboratory of Tree-Ring Research were most cooperative in providing support for the workshop. Marna Thompson, Terry Mazany, and Tom Harlan handled many of the arrangement and organizing details for the workshop.

Special thanks to Phyllis West, Rocky Mountain Forest and Range Experiment Station, Tempe, AZ. for her clerical and manuscript assistance during the workshop, and to John McKelvy, Fire Management Officer, Santa Catalina District, Coronado National Forest for his efforts in hosting the field trip to Mount Lemmon.

Marvin Stokes

J. H. Dieterich

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The Dendrochronology of Fire History[1]

M. A. STOKES[2]

Abstract.--Dendrochronology, the study of annual rings in woody plants, has developed into a useful tool for a number of different fields of study. Based on the interaction of trees and the climate, it is possible to use tree-rings as proxy data in reconstruction of past climates and river runoff. It has been a dating tool of archeologists. The value of dendrochronology in fire history research has the potential of providing important data over and beyond the dating of fire scars.

The principles and practices of dendrochronology were developed in the American southwest by Dr. A. E. Douglass, an astronomer. When he first began his study of tree-rings, he was looking for a tool to be used in the study of sunspot cycles and their relationship to the earth's climate. From the late 1890's to his death in 1962, this remarkable scientist developed the science of dendrochronology and applied his keen mind to the various applications of tree-ring studies. The first application was to the climatic record contained in tree-ring series. In the 1920's, the use of tree-rings as an archeological dating tool began, culminating in 1929 in the establishment of a precisely dated archeological tree-ring chronology. This is a continuing viable aspect of dendrochronological research. During the 1930's and 1940's, Douglass continued to expand the time series boundaries in his search for old age trees. This work, carried on by Dr. E. Schulman, resulted in the establishment, on a sound basis, of tree-rings as a valid estimate of past climates (Douglass, 1919), leading to the application now called dendroclimatology (Schulman, 1956). This period in the history of tree-ring research also saw the application of tree-ring time series to the study of fluctuations of river runoff (Schulman, 1945), another very active line of continuing research (Stockton, 1975).

The interaction of tree growth and the climatic environment in which the tree grows is the basis of all tree-ring research, the unifying element of all applications. The basic principles governing dendrochronology are summarized below (Fritts, 1976):

1. Limiting factor: The biological process of ring growth cannot occur at a faster rate than allowed by the most limiting factor affecting that process. In the southwest, the most limiting factor is that of precipitation (available soil moisture) acting in combination with temperature In other areas, different agents may be more limiting.

2. Well defined growth layer: The expression of growth in the tree must be well defined (a tree-ring) and the duration of growth must be known, such as the annual ring.

3. Site selection: While all trees are affected by the climatic environment, as well as the biotic, certain trees will reflect the limiting factor more than others. Thus trees growing at the lower forest borders, in semi-arid environments, will show the greatest effects of the limiting factor to the maximum extent.

4. Sensitivity: Because the limiting factor varies through time, the widths of the annual rings will reflect such a variation. Trees that have a highly variable ring width series are considered to be sensitive; those that show little variation in ring width from year to year are considered to be complacent.

5. Cross dateability: Cross dating is the matching of a ring pattern of wide and narrow rings from one specimen to another, such matching establishing the synchronaeity of the rings. Since trees in a given area are influenced by a common fluctuating limiting factor, similar ring patterns will be produced in the trees. This cross dating is what makes the precision of tree-ring dating a reality, and is an absolute essential in order to "date" a tree-ring or a series of tree-rings. Starting with the known date of the most recently formed growth layer, the previously formed rings, in sequence, can be correlated with the calendar year of formation. Several problems can be present, however. Absent rings in a given specimen must be

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[1] Paper presented at the Fire History Workshop, Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980.

[2] M. A. Stokes is Professor of Dendrochronology, Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz.

identified by comparing with ring patterns of other specimens. "False rings", anomalous growth bands which do not represent total growth for any one season, must also be identified in the cross dating procedure.

6. Verification: So that complete confidence may be placed upon the cross dating procedure, a sufficient number of specimens must be studied to insure that all problems have been eliminated from the dated tree-ring series. For those trees with a greater frequency of absent rings, a larger sample size is required. In our research in the Laboratory of Tree-Ring Research, a minimum number of two cores per tree from at least ten trees which are dateable and sensitive has been established as basic for developing our tree-ring chronologies. Hundreds of chronologies have been developed in the past two decades, and are published in a series of Laboratory publications (Stokes, et al, 1973; Drew, 1976). These chronologies cover the western United States, some parts of the mid-west, parts of Canada and northern Mexico. They constitute a very valuable library of basic data available for many different types of research, including the study of fire history in forest communities.

The techniques of the actual process of tree-ring dating will not be covered here. The preparation of specimens for dating, skeleton plotting, cross dating, and verifying cross dating are techniques best learned by actual practice (Stokes and Smiley, 1968).

As was stated previously, the interaction of tree growth and the climatic environment and its expression of that interaction in the varying ring widths is the basis for dendrochronology. Other factors, however, are superimposed upon that interaction. One of the factors, the one we are interested in here, is that of fire. The most obvious evidence, of course, is that of the scar resulting from fire. Our immediate interest is to date the fire scars in order to determine some frequency of the fire events, prior to the application of management practices in our forests. Such information is of the utmost importance if we are to incorporate fire as a management tool, and if we wish to determine whether fire is an important part of the total picture of forest ecology. I will cover, briefly, some aspects of dating fire scars and then discuss some further implications.

Dating a fire scar would seem to be relatively simple: it "dates" according to the ring it is in. The dating of the ring(s) is not done along the two radii of a fire scar, however. To insure the precision of dating, a radius must be selected that is far enough removed from the distortion of ring widths caused by either the fire itself or the subsequent healing process. Therefore, I feel a cross section of the tree stem is necessary for fire scar dating, and the radius selected should be approximately at right angles to the face of the scar. Any discontinuity of the ring series due to "absent rings" can best be worked out along that relatively undistorted radius. Even though the sample may represent a compacent ring series, absent rings along the fire scar face may result in the loss of the precision you seek (see illustration in Fritts, 1976). If working with species of trees that has not been extensively studied by dendrochronological techniques, the absent ring problem is again a real risk (Jordan, 1966).

I think we all recognize the importance of sampling both sides of a fire scar. The discrepancy of dates between two sides of a scar can be very great and any frequency estimate based on only one scar radius can be very misleading.

The definition of a fire caused scar is something that bothers us here in the Tree-Ring Laboratory. The criteria we have been using are somewhat uncertain. The presence of charcoal in the wound is the first criterion. The observation of subsequent healing over the area of wounding is the second criterion, and the presence of vertical lines representing the healing from the sides of the scar is the third criterion. But a succession of fires may very well eliminate or obscure evidence of earlier fires and make it difficult to determine whether a "scar" is actual evidence of an earlier and separate fire event. Any of a combination of two of the above criteria is probably accurate, but an element of doubt remains. A fourth criterion may be used but we have not quantified this, as yet. In some cases we have observed a band of what appears to be disrupted cells, within the growth ring, at right angles to the scar face. When the origin of the scar is uncertain, this condition may indicate the presence of heat causing either a disruption of cellular tissue or some change in cellular constituents.

A discrepancy in dates between the two sides of a fire scar has been observed. Where the discrepancy between two opposite scars is a difference of one year, the error may very well be in determining in which ring the scars occur. However, do differences of two, three or even four years represent specific fire occurrences? The elminiation of these slight differences may mean quite a change in the frequency interval obtained. Some caution must be used, until this question is resolved. In summary, all scars which show the curved growth of lateral healing are the most positive indicators of fire events. All others, while they may have certain characteristics which seem to indicate a fire origin, have an element of doubt.

To establish fire frequency, based on dating of fire scars, is a first step in a potentially rewarding line of tree-ring research. If we might, let us speculate a bit. Assuming that fire was part of the forest ecosystem in the past, and occurred at some frequency, what more information may be contained in the tree-rings that would allow you to refine the results now obtained through fire scar dates? Arno and Sneck (1977) pose a question, among others, of what are the effects of past fires on the forests. In growth response studies done in the Laboratory by Fritts and his workers, the climatic parameters of rainfall and temperature are used as independent variables in studying the relationship of tree growth and seasonal changes of the climate. The tree response to fire occurrences may very well be revealed by using fire history data as another "independent" set of nonclimatic variables to plug into growth response studies. Using response function analysis, reconstruction of past fire histories, in terms of increased growth or decreased growth, may be possible. Fire, of course, is not independent of climate, and the characteristics of fire are not independent from the characteristics of the forest community it occurs in. Further research will allow us to better define the relationships involved in the tripart system of

Climate

Tree growth Fire

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Fire History of a Mixed Conifer Forest in Guadalupe Mountains National Park[1]

Gary M. Ahlstrand[2]

Abstract.--Fire scarred southwestern white pine (*Pinus strobiformis*) cross sections from a 1700 ha study site in the Guadalupe Mountains were examined to determine the historic role of fire in the forest. At least 71 fires have occurred on the site since 1554. The mean interval between major fires was 17.4 years for the period 1696-1922. No samples were scarred after 1922. Reduced incidence of fire during the past century coincides with changes in occupancy and use patterns in the mountains.

INTRODUCTION

Tree stems with multiple fire scars are evidence that fire has been a significant ecological factor operating in the past on a relict mixed conifer forest in the high country of Guadalupe Mountains National Park, Texas. The historic role of fire in this ecosystem was little understood, however. The absence of fire in the recent past has permitted thickets of conifers to become established in the understory throughout the high country. It was not known if this represents a natural phase in the life cycle of the forest, or if it resulted from European man's activities in the area during the past century.

Little information concerning fires in the forest was readily available. Robinson (1969) reported that fires occurred in the forest in approximately 1858 and again in 1908 or 1909. A native that has resided west of the park since 1906 recalled having seen flaming trees fall from high cliffs in the mountains in about 1909 and smoke from another fire in the high country in about 1922 (E. Hammock, personal communication). No fires of any consequence have been reported for the forest since 1922.

This study was conducted to determine the fire history for a portion of the relict mixed conifer forest. Cross sections from fire scarred tree stems were studied in an attempt to identify specific fire years, the incidence of fire in the study area, the fire free interval for specific small areas within the study area, and a general indication of past fire intensities. Changes in the role of fire resulting from shifting patterns of use in the forest are also addressed.

STUDY AREA

The study area consists of approximately 1700 ha in the upper portion of the South McKittrick Canyon watershed in Guadalupe Mountains National Park (fig. 1). The area sampled ranged in elevation from 2150 to 2550 m and included the most heavily visited portion of the park's high country.

The semiarid, continental climate of the area is characterized by mild winters, warm summers and summer showers. Lightning ignited fires occur mainly during spring or early summer before the onset of showers that accompany summer monsoons.

Associates in the mixed conifer forest include Douglas-fir (*Pseudotsuga menziesii*), southwestern white pine (*Pinus strobiformis*), and ponderosa pine (*Pinus ponderosa*). Dry, south-facing slopes support an open woodland of ponderosa pine, alli-

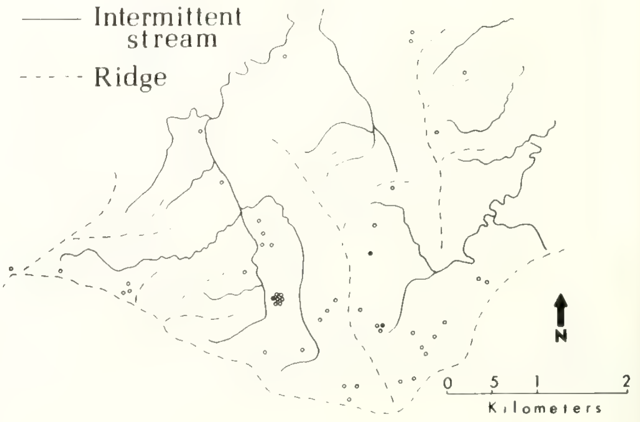

Figure 1.--Map of the Guadalupe Mountains high country study area showing locations of sampled live cut (●) and dead (○) fire scarred stems.

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[1] Paper presented at the Fire History Workshop, Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980.

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gator juniper (*Juniperus deppeana*) and pinyon pine (*Pinus edulis*). Where soil moisture is more available, as on slopes with some northerly aspect, Douglas-fir and southwestern white pine dominate, with ponderosa pine and pinyon pine included in the association.

Indians are known to have occupied the area, at least seasonally, until about 1870. By the middle of the 19th century, parties of soldiers, surveyors, settlers and gold seekers were passing through the area on a trail just south of the Guadalupe Mountains. European settlers were in the area by the 1870's. By the turn of the century, cattle, horses, sheep and goats were being run on rangeland surrounding the mountains, and even in the high country (E. Hammock, personal communication). Use of the high forested country for summer range continued into the 1960's, but was phased out between 1966 and 1970 after Congress authorized the area to become a national park. The area was officially dedicated and established as a national park in September 1972.

METHODS

Knowledge of the fire history for the relict forest was considered important enough to justify cutting cross sections from a number of fire scarred stems. Transects were laid out in the study area as described by Arno and Sneck (1977). Forty-eight stems, all southwestern white pine, have been sampled to date (fig. 1). The cross sections came from 3 living stems, 36 standing dead stems, 3 fallen dead stems, and 6 stumps left when a trail was widened through a portion of the study area. The location of each sample was noted on a 7.5 minute topographic map.

A master tree ring chronology was constructed from indices calculated from measurements of annual rings in two increment cores from each of 19 Douglas-fir trees (Fritts 1974). The master chronology was used to cross date the fire scarred sections. When a sample section predated 1668, the earliest date of the master chronology, a ponderosa pine chronology from Cloudcroft, New Mexico dating to 1515 was used (Drew 1972).

Annual rings in the samples were measured under 30-90X magnification on a sliding stage micrometer to the nearest 0.01 mm. Widths of annual rings were plotted chronologically with fire scarred rings noted. The sample plot was then cross dated with a plot of the master chronology.

Some fire scars were so distinct that it was possible to identify the fire as having occurred during the early, middle or late portion of the growing season for a particular year from the number and size of xylem cells formed prior to injury of cambium. When scars appeared to have formed between growing seasons, it was assumed that the fire occurred during the dry, winter-spring season unless a scar on a sample from a more sheltered site indicated that the fire burned late in the previous year's growing season. Occasionally a fire scarred ring was obscured by partial loss of the ring in a subsequent fire, or decay. Such rings were included only when they could be cross dated with reasonable certainty within one year of another scarred stem from the vicinity.

When feasible, two or more fire scarred stems were sampled in a small area as in similar studies (Houston 1973, Arno and Sneck 1977, Kilgore and Taylor 1979). The occurrence of fire was determined for two approximately one hectare sites. Seven stems located within 100 m of each other were sampled on a west-facing slope near the crest of a ridge, and three cross sections from stems that had grown within 100 m of one another were taken from a north-facing slope near the bottom of a small ravine.

A fire year was defined as any year in which at least one sample was scarred by fire. Major fires were defined as those in which 20 percent or more of the samples alive at the time of the fire were scarred, and at least two of the scarred samples must have been separated by a minimum of 2 km.

All trees in fifteen 25 X 15 m plots were recorded by species and to the nearest diameter at breast height (dbh) size class. Size class 1 included all stems less than 1 m tall; size class 2 included stems less than 5 cm dbh; size class 3 consisted of stems 5-10 cm dbh; and successive size classes increased in 10 cm dbh increments. Increment cores were taken from representative stems of Douglas-fir and southwestern white pine so that each size class could be correlated with tree age.

RESULTS AND DISCUSSION

Data from 305 fire scarred annual rings contained in 48 southwestern white pine cross sections indicate that fires of various sizes have occurred in the study area in at least 71 of the years between 1554 and 1980 (fig. 2). Sixty-three of the fires occurred before 1850 and none of the cross sections were scarred by fire after 1922. The number of fires per cross section ranged from 2-14 and the mean

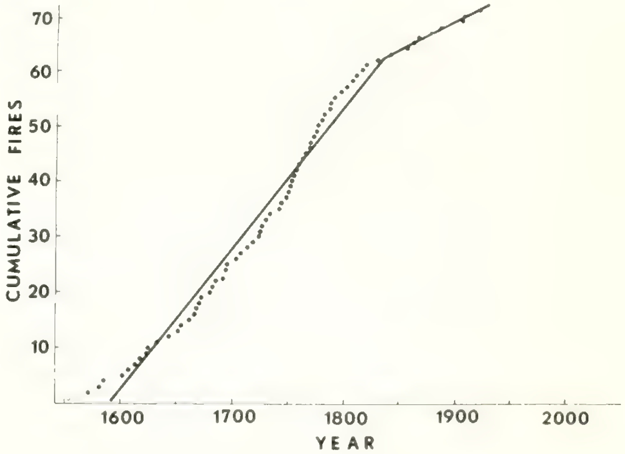

Figure 2.--Incidence of fire in the study area as determined from fire scarred sample stems. Parameters for the regression line are: 1554-1842 segment, $y = 0.251x - 399.8$, $r = 0.986$; 1842-1922 segment, $7 = 0.0995x - 120.2$, $r = 0.993$.

interval between scars for individual cross sections varied from 11.5-68.3 years.

Because no stems were scarred by every fire, the occurrence of fire is undoubtedly more frequent than indicated by the data. For example, 19 fires were represented by 35 scars that occurred in seven cross sections taken from one of the hectare sampling sites. Eleven of the fires were represented by only a single scar in the sample. Two fires each scarred four stems and the maximum number of stems scarred by any fire was four. The 19 fires occurred between 1673 and 1922. During this period the interval between fires ranged from 3-45 years and the mean fire free interval was 13.8 years. Fires scarred the three sample stems from the other hectare site in 21 of the years between 1643-1879. The fire free period ranged from 2-37 years during this period and the mean interval between fires was 11.8 years.

The mean interval for the incidence of all fires detected in the study area for the period 1554-1842 was 4.7 years (fig. 2). Between 1842 and 1922 the fire free interval more than doubled. None of the sample stems were scarred by fire during the last 58 years.

Between 1696 and 1922, 14 major fires occurred in the study area (fig. 3). The interval between major fires ranged from 6-30 years, and the mean interval was 17.4 years.

The reduced incidence of fire apparent after 1842 coincides with the ever increasing impact of European man and the decreasing presence of Mescalero Apache Indians in the area. By 1880 most of the Indians had been driven from the Guadalupe Mountains. This suggests that many ignitions in the forest prior to the mid-1800's were associated with the use of fire by Indians. The high country most likely received limited use between 1880 and the early 1900's as European man settled in the area.

Until this century, 30 years appear to have been the maximum interval between major fires in the study area. Thirty years elapsed between major fires that occurred in 1879 and 1909. The last major fire to occur in the study area was in 1922. Increased use of the high country after 1930 as summer range for livestock probably prevented cured grasses from accumulating in quantities sufficient to carry a fire any great distance. Longtime residents recall that although the forest understory was open and park-like as recently as the early 1950's, large numbers of conifer seedlings were becoming apparent about this time, nearly 30 years after the last major fire.

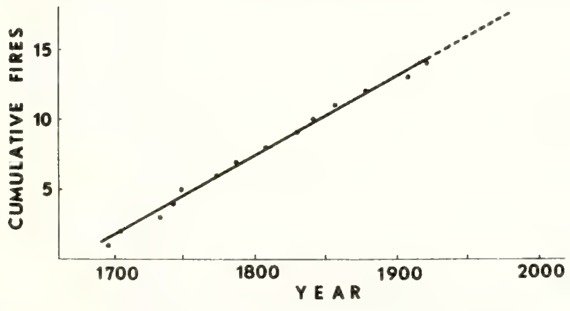

Figure 3.--Occurrence of major fires in the study area, 1696-1922. Parameters for the regression line are: y = 0.0566x - 94.55, r = 0.996.

A fire suppression policy has been in effect for the area since coming under the stewardship of the National Park Service. One ignition burned undetected in 1974 on an open, southwest-facing slope in the study area. Less than two hectares were burned before the fire died, and no trees were found to have been scarred as a result of the fire. Other fires originating outside the study area might have spread into the area had they not been contained by fire suppression crews while still small.

Most of the fires in the relict forest appear to have been relatively low intensity ground fires. Scarred stems in the forest are predominately those of southwestern white pine. Fire scarred stems of the more heavily barked Douglas-fir and ponderosa pine were seldom encountered. Fire damaged stems of young southwestern white pine usually die, and older trees remain susceptible to scarring for many years. Only three of the samples were scarred when less than 15 years old. Nearly half the sample stems were more than 50 years old when first scarred by fire.

Pooled size class density data for southwestern white pine showed fewer trees present in size class 3 than would normally be expected (fig. 4). Southwestern white pines of this size class in the study area are ordinarily 50-100 years old. A similar pattern was noted with Douglas-fir, except that both size classes 3 and 4 contained fewer trees than would be expected in a regular distribution (fig. 5). Comparison of age data from

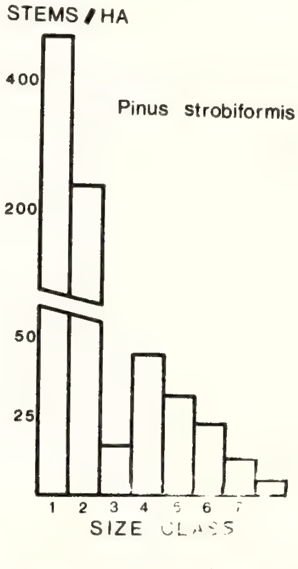

Figure 4.--Density of southwestern white pine by size class in the mixed conifer forest, Guadalupe Mountains National Park, Texas. Size classes are: 1 = stems < 1 m tall; 2 = stems to 5 cm dbh; 3= stems 5-10 cm dbh; and successive classes increase in 10 cm dbh increments.

increment cores with diameter data for both species indicate that growth rates for Douglas-fir in these size classes slightly exceed those for southwestern white pine in the study area. Many of the trees expected in these size classes in a normal distribution were apparently destroyed by the 1909 fire. During the 30 year interval since the last major fire in 1879, fuels probably accumulated tc levels that supported a more intense than usual fire. Most of the trees in size classes 1 and 2 became established after the last major fire to occur on the study site in 1922. Dense thickets of Douglas-fir have become apparent in the last 25-30 years (fig. 5).

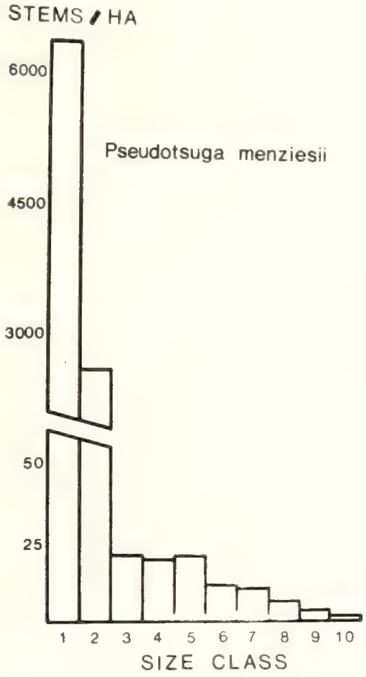

Figure 5.--Density of Douglas-fir by size class in the mixed conifer forest, Guadalupe Mountains National Park, Texas. Size classes are the same as for figure 4.

Data from this study indicate that the mixed conifer forest was overdue for another major fire by the mid-1950's. Many of the stems that now contribute to the dense understory thickets would have been destroyed had a fire occurred. A critical situation exists in the forest today. Ignition under certain weather conditions with the present dead and living fuel accumulation could result in a devastating fire. Perpetuation of mixed conifer forest is dependent upon finding an effective means to reduce fuel loads while saving most of the trees in the canopy.

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The Composite Fire Interval — A Tool for More Accurate Interpretation of Fire History[1]

J. H. Dieterich[2]

Abstract.--Use of the Composite Fire Interval (CFI) as a means of expressing historical fire frequency for a particular area is discussed. Four examples are presented that summarize historical fire intervals on areas ranging in size from 100 to several thousand acres.

INTRODUCTION

A wide range of methodologies is available for documenting fire histories in various timber types using fire scars and dendrochronology techniques (pyro-dendrochronology). Early work by Clements (1910) described a method of determining fire history in the lodgepole pine (Pinus contorta) forest of Colorado. Weaver (1951) studied fire history in the White Mountains of Arizona and identified individual tree average fire intervals ranging from 4.8 to 6.9 years. He was perhaps the first student of fire history to establish contact with the Laboratory of Tree-Ring Research, University of Arizona, for the purpose of cross-dating and verifying the dates of fire-scarred material from ponderosa pine (Pinus ponderosa).

More recent pyro-dendrochronology studies by Heinselman (1973), McBride and Laven (1976), Arno and Sneck (1977), Alexander (1977), Wein and Moore (1979), Zackrisson (1977), Rowdabaugh (1978), Kilgore and Taylor (1979), Tande (1979), and Dieterich (1980) have utilized a variety of approaches to analyzing fire history in specific forest types. Most of these studies further described the ecological changes that have resulted from the elimination of natural fires through improved fire suppression organization.

In 1975 we were preparing plans for a long-term prescribed burning study designed to evaluate the effects of using fire at various intervals on fuel accumulation and consumption. We knew that fire had been an integral part of the southwestern ponderosa pine ecosystem for centuries but we were searching for scientific information that would suggest what burning intervals would be reasonable for us to incorporate into the studies. The work by Weaver (1951) was the only information available on fire history in southwestern ponderosa pine. To expand Weaver's findings, and establish a basis for interval burning, we collected fire-scarred material from the site we had selected for our long-term prescribed burning study, and, started a regional collection of fire-scarred material from the national forests of Arizona and New Mexico.[3] The Forest Service, Region 3, Division of Timber Management sent out instructions for severing cross sections from fire-scarred trees taken from current or recently active timber sales. The cross sections were sent to the Laboratory of Tree-Ring Research for dating and verification.

Site cards were prepared for each sample, and the location of each specimen was plotted on a map. In an effort to detect a pattern in the data, fire dates from each specimen were plotted on a common chart. This "composite" as it came to be called wasn't as useful as we had hoped because it covered such a large area. However, it did reveal some periods of years when fires appeared to be more common, and more importantly, it suggested a methodology that could be used to look at fire history on smaller land units.

The collection for the Chimney Spring study site and the preparation of the Composite Fire Interval (CFI) for the site is described in a recent research paper (Dieterich 1980).

Before proceeding further, the Composite Fire Interval concept and some of the criteria involved in its development should be discussed. A CFI is a means of more accurately expressing historical fire frequency for a particular area. It involves collecting at least two (preferably more) fire-scarred cross sections, and determining dates of fire scars by cross-dating and verification of the tree-ring material using an established tree-ring chronology.

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[1] Paper presented at the Fire History Workshop, Tucson, Arizona, October 20-24, 1980.

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[3] Fire histories in southwestern ponderosa pine. 1975. Study plan on file, Rocky Mountain Forest and Range Experiment Station, Tempe, RM-2108.

Size of the area represented by a CFI is important but difficult to specify. The concept seems more appropriate for describing fire history on relatively small areas (such as historical sites, research plots, experimental watersheds), and seems more useful when there is a uniformly high level of fire occurrence. We have used the procedure to develop fire histories in southwestern ponderosa pine and mixed conifer types.

To determine a CFI, dates are plotted on a chart that spans the total number of years represented by the collection of fire-scarred specimens. This visual display of "fire years," along with center-ring dates and dates of outermost rings, makes it possible to identify dates from the various specimens that are common to one another, inspect for gaps in the fire sequence data, and identify periods of years having maximum fire frequencies.

Use of the CFI for describing fire histories on four different areas in northern Arizona and southern Colorado is discussed in this paper. In addition to preserving valuable historical information the CFI provides a scientific basis for speculating on the types and extent of plant and animal communities that existed in centuries past, and an opportunity to evaluate present day fuel and vegetative conditions in terms of past fire history.

EXAMPLES OF COMPOSITE FIRE INTERVALS

Chimney Spring

In reviewing the Chimney Spring fire history, it is appropriate to restate some basic assumptions regarding fire behavior and fire spread (Dieterich 1980).

1. A fire starting within the general area where the samples were taken would have had a good chance of spreading over the entire area.
2. A fire spreading into the area from outside would also have spread over the entire area.
3. These fires would not necessarily have burned every square foot of surface area because of fuel discontinuity, thus leaving some trees unscarred with each passing fire.

These assumptions also appear valid for the Limestone Flats study area but probably do not apply to the Thomas Creek fire history study area to be discussed later in this paper.

Significant results from the Chimney Spring fire history study are:

1. The most recent fire on the area, confirmed by scars on five of the seven specimens, was in 1876.
2. The oldest fire scar was recorded in 1540 (Tree 7).
3. Fires occurring at 2-year intervals were recorded five times on Tree 6 and once on Tree 7. There were no instances where fires were recorded in successive years.
4. The CFI for the 122-year period, 1754-1876, was 2.4 years. All seven specimens were represented in this CFI.
5. The most intense CFI (1.25 years) was recorded for the 15-year period (1850-1865).
6. Adjacent trees (6 m) revealed a number of common fire scars (11) and nearly an equal number of fire scars (12) that were not in common.

Results from the Chimney Spring fire history study assure us that the prescribed burning intervals we chose (1, 2, 4, 6, 8, and 10 years) are appropriate and represent a realistic range of intervals for using prescribed fire. This fall we will be applying fire for the fifth consecutive year on the Chimney Spring annual-burn plots; we will be burning the 2-year interval plots for the second time; and we will be burning the 4-year plots for the first time since the initial fuel reduction burn in 1976.

Limestone Flats

This is a companion study to the Chimney Spring prescribed interval study. Objectives of the study, plot design, timber type, and burning intervals for the two areas are the same. The primary difference between the two areas is the soil type, although there is also a small difference in elevation (500 feet ±). Chimney Spring parent material is basaltic; Limestone study site is limestone-sandstone. The Limestone plots are located 50 miles south of Flagstaff, 8 miles from the southern edge of the Mogollon plateau. Lightning fires are common in the area, there have already been two lightning fires on the 100-acre study site in the past 3 years.

Figure 1 shows the approximate location of fire-scarred material being used to construct the CFI for the Limestone Flats study site. Trees with fire scars are reasonably well distributed on the area. Specimens 4 and 12 have been collected but as yet have not been dated. Fire dates from these specimens will be added to the CFI when they become available.

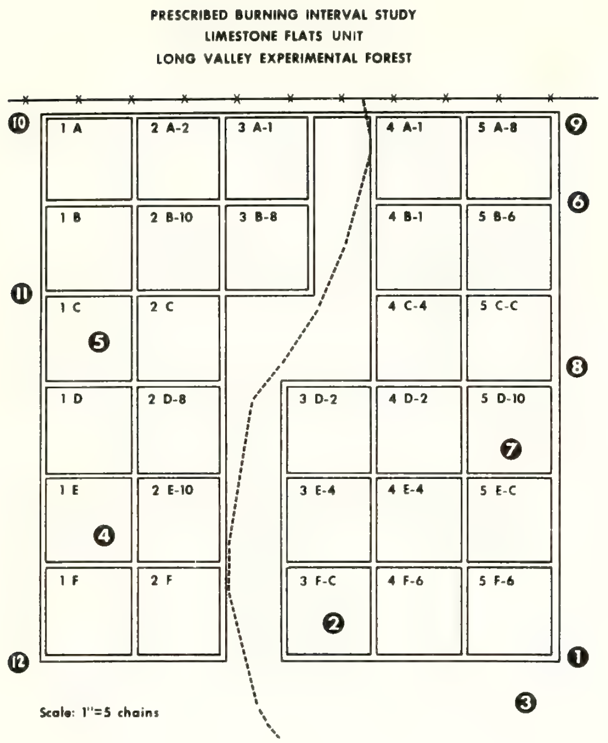

Figure 1.--Limestone Flats prescribed burning interval study plots showing approximate location of fire-scarred trees used for reconstructing fire history for the area. A narrow access road divides the plots but physiographic conditions are similar on both sides.

Figure 2 is the CFI for the 110-year period (1790-1900) on the Limestone study site. The total time-span represented by all the fire scar material covers more than 300 years but only the central portion has been used. Prior to 1790, 21 fire-years were identified on available fire-scarred material dating back to 1722. Only five fire-years have been recorded on the area since 1900. Further interpretation of the fire history from the CFI for the 110-year period indicates the following:

> Nine out of the 10 specimens were available to contribute to the CFI for the area beginning in 1790. Specimen 7 was available in 1851. The CFI for the 110-year period 1790-1900 is 1.8 years (61 fires; 110 years). For the 50-year period 1810-1860, the CFI was 1.3 years. There were 25 fire-years on the area between 1810 and 1841 for a CFI of 1.2 years.

If it had been possible through some prior knowledge to select the "best" trees for fire history analysis purposes a relatively few samples would have been needed. For example, if only specimen 2 had been used the average fire interval would have been identified as 4.1 years. If only trees 2, 3, and 5 had been used to prepare the CFI for the 110-year period 1790-1900 the interval would be 2.4 years--only slightly longer than the CFI based on all 10 specimens for the same period.

In an effort to gain a somewhat different perspective of the fire history on the Limestone Flats study area, a short movie has been assembled to show the area as it looked both before and after the initial fuel reduction burn in 1977, and provide a visual display of fire activity on the area during the 110-year period from 1790-1900.

Located at an elevation of about 6,900 feet the stand is typical of old-growth undisturbed ponderosa pine--essentially uneven-aged with small even-aged groups. There are patches of stagnated saplings, small and large pole stands, and groups of old-growth yellow pine scattered throughout the area. A light sanitation cut was made on the area about 15 years ago. One or two large trees per acre were removed and scattered snags were dropped. Basal area averages 121 square feet per acre with individual plots ranging from 91 to 169 square feet. Site index averages about 72.

Before burning, fuel loading of material under 1-inch diameter (needles, twigs, litter, etc.) averaged 16 tons per acre; woody material over 1 inch in diameter averaged 16.5 tons per acre for a total fuel loading of 32 tons per acre (Sackett 1980). The last fire to burn over the area was in 1898; fire scars from 1928 and 1930 were found on two specimens.

The first fire occurrence display (1790) shows the location of nine of the specimens used to compute the CFI. During that year, two of the trees (5 and 10) were scarred by fire.

The succeeding years show the number of trees that were scarred and their location. I have arbitrarily (but conservatively) estimated that if two or more of the trees sustained scars, there was a good chance that the entire area burned over, although not necessarily every square foot within the area. If this estimate appears reasonable, it is likely that the area burned over at least 32 times during the 110-year period. However, if we accept the basic assumption as stated for the Chimney Spring site, the entire area would have burned over 61 times or each time one of the specimen trees was scarred.

To summarize for the Limestone Flats study area, inspection of the CFI data leads to the following conclusions:

- The prescribed burning intervals selected for the study appear to be realistic in terms of past fire occurrence;
- The fuel loading on the area in 1900 was vastly different from what was present when the plots were burned in 1977.
- Fine fuels (grass and needles) would have been the medium through which these historical fires spread because most large fuels would have been consumed by the frequent fires;

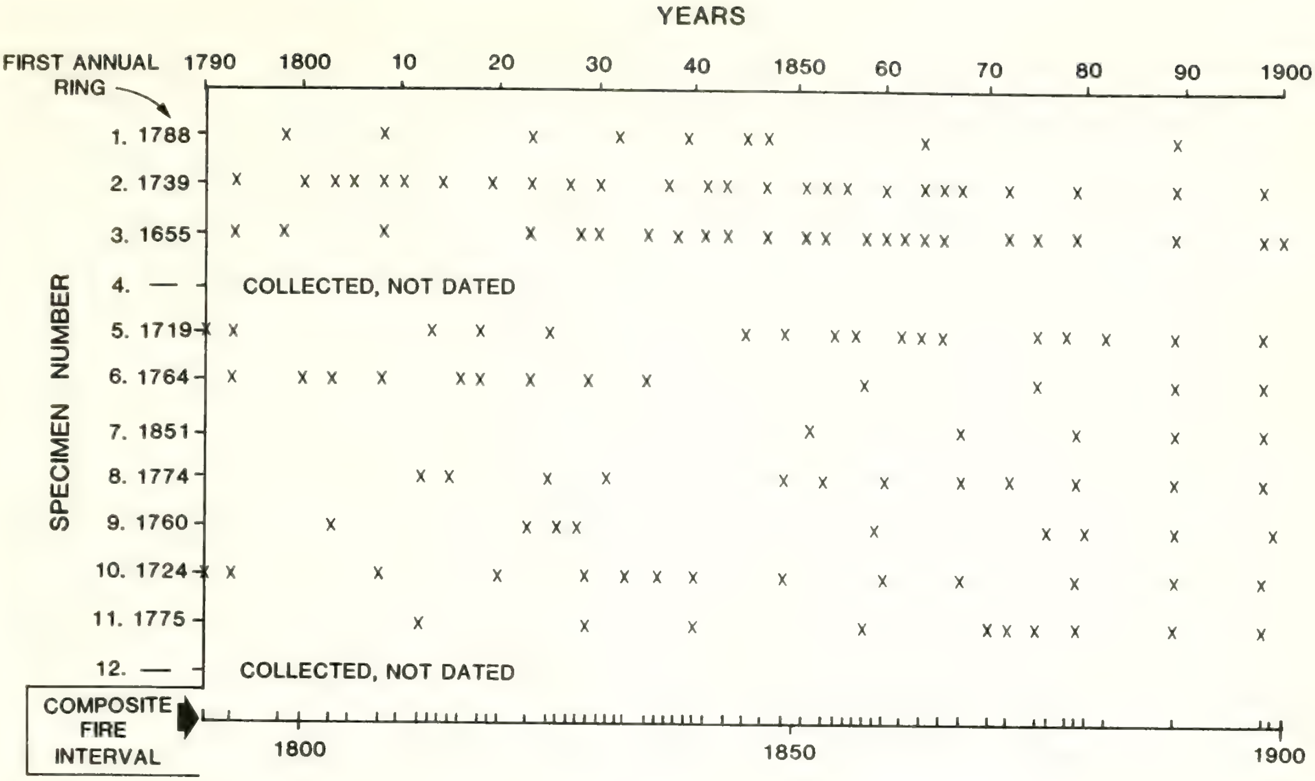

Figure 2.--Composite Fire Interval for Limestone Flats prescribed burning study plots. Time span: 110 years; "Fire-Years": 61; Composite Fire Interval: 1.8 years.

- The dense thickets of stagnated pine saplings would not have been present prior to 1900 due to the frequent occurrence of surface fires;

- And, while many seedlings and young trees would have been destroyed by these frequent low-intensity fires, enough would have remained to maintain stocking within the stand.

Thomas Creek

In contrast to the ponderosa pine histories for Chimney Spring and Limestone Flats, fire history findings on the Thomas Creek experimental watershed reflect differences in elevation, stand type, and species composition.

Thomas Creek is part of a water yield improvement study located on the Apache-Sitgreaves National Forest near Alpine, Arizona.[4] Elevations range from 8,300 to 9,200 feet; the stand is typical of undisturbed southwest mixed conifer. Precipitation averages 28 inches per year. Tree species include ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), southwestern white pine (*Pinus strobiformis*), corkbark fir (*Abies lasiocarpa* var. arizonica), Engelmann spruce (*Picea engelmannii*), and aspen (*Populus tremuloides*). Douglas-fir and white fir are the main understory species and make up about 50% of the trees and 55% of the basal area, which averages about 190 square feet.

The watershed was scheduled for a treatment in 1976 and a cut was prescribed designed to increase water yield while protecting wildlife and recreational values. Marking guides limited volume removal to about 30% of the basal area--mostly in individual trees or small groups.

Fire scars were present on a large number of old-growth trees of nearly all species. Arrangements were made prior to cutting to have specific trees designated as "fire history" trees. The loggers were asked to "high-stump" these trees so that a slab could be removed later for study. Fire history trees were selected on the basis of location with respect to other fire-scarred trees to insure a good sampling distribution over the area. Trees with numerous scars evident on the "catface" were also favored in the selection process. Fire-scarred specimens taken on Thomas

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[4] Core Study Plan, Thomas Creek Resource Evaluation Project. April 25, 1975. Rocky Mountain Forest and Range Experiment Station, Tempe, RM-2108.

Creek were principally ponderosa pine, but a number of white pine cross sections were also removed for study. These two species scar readily and resisted decay better than other species scarred by fire. Six "pairs" of specimens were chosen (ponderosa pine-white pine), for comparing the incidence of scarring in the two species to determine if one species scarred more readily than the other. This analysis is as yet incomplete.

A total of 34 specimens were collected from this area of approximately 420 acres (170 ha). Cross-dating and verification is being done by the Laboratory of Tree-Ring Research. Results of the study are incomplete and will be published at a later date, but preliminary findings indicate the following:

1. The most recent fire scar recorded was in 1911. There have been few fires since 1900.

2. The preliminary CFI chart revealed widespread scarring on the watershed in 1748, 1819, 1847, 1873, and 1893. Further analysis of data should confirm these years and may reveal additional years when fires apparently covered the entire watershed.

3. The CFI is longer on Thomas Creek than on the Chimney Spring or Limestone areas. During normal years in the mixed conifer type fire weather is not as extreme and, although lightning may cause frequent fires, they spread slowly in the damp fuels and frequently go out. This type of fire created scars on some of the trees, as indicated in the CFI, but probably did not spread over a large area.

4. Perhaps the most significant finding is that, in spite of frequent fires, some extensive enough to cover the entire watershed, the area remains as a mixed conifer type. This is an important concept because to date silviculturists have maintained that fire and the mixed conifer type are not compatible.

San Juan National Forest

In 1975, 10 fire-scarred cross sections were collected from scattered stands of ponderosa pine on the San Juan National Forest in southern Colorado. Forest personnel were starting on a prescribed burning program to reduce natural fuel buildup, stimulate natural regeneration, and hold back invasion by Gambel oak (Quercus gambelii), a competing understory species. They therefore needed to know about the frequency of historical fires.

The 10 specimens used for this CFI came from three different Ranger Districts on the Forest. They were forwarded to the Tree-Ring Lab in Tucson for cross-dating and verification. Results are as follows:

1. Individual tree average fire intervals ranged from 7 to 35 years.

2. The most useful fire history data came from the 150-year period 1750-1900. There were 38 fire-years during this period for a CFI of 3.9 years.

3. Within the above period the 85-year span 1815-1900 yielded 25 fires for a CFI of 3.4 years; and for the 50-year period 1840-1890, 22 fire-years were recorded for a CFI of 2.3 years.

Because of the widespread location of the sample trees, the CFI was not necessarily representative of any particular site. However the range of CFI's (2.3, 3.4, 3.9 years) computed for 22, 50, and 150 years respectively provided the Forest with useful information for expanding their prescribed burning program.

DISCUSSION

An important limitation of the CFI is the lack of statistical control resulting from an indeterminate number of samples taken from an area of unspecified size. On undisturbed areas of old growth trees there is usually ample material available for developing good composite fire histories. On cutover areas where fire damaged trees have been removed, available material may be limited to old stumps or fire-scarred material scattered over the area.

The CFI provides an indirect measure of fire intensity. Knowing fuel type, loading, and arrangement, and knowing the natural fire frequency as indicated by the CFI, a reasonable estimate can be made of fire intensity--at least in relative terms. Low intensity fires must have been common, and high intensity fires unlikely, because frequent fires maintained fuel volumes at low levels.

While not necessarily a limitation of the CFI system, it is difficult, if not impossible, to reconstruct fire size and perimeter for historical fires in southwestern ponderosa pine because of the uneven-age character of the stand, and the fact that fires occurred so frequently. For example, the fact that two trees located "X" miles apart show fire scars for the same year does not mean that the entire area between the sites burned. In fact, the character of the fuels present at that time (mostly grass and fresh litter) would have precluded extended spread over a several day period. Light fuels would respond to slight increases in fuel moisture, thereby limiting spread over large areas.

Exclusion of fire in the stands where ponderosa pine is considered climax does not appear to have resulted in any significant changes in the overstory species composition. Although understory vegetation and age-class distribution of ponderosa pine stands have probably changed. An optimum combination of seed source and weather around 1919 resulted in the establishment of dense stands of reproduction over large areas (Schubert 1974). Around the turn of the century the natural fire interval had been interrupted, largely as a result of extensive grazing by livestock (Dieterich 1980). Without the influence of periodic natural fires, and in the absence of prescribed burning, these areas of reproduction developed into stagnated stands that today occupy in the neighborhood of some 3.5-4 million acres. These stands pose a significant problem for the land manager in that they are a serious fire hazard, are occupying productive sites, and are expensive to thin or otherwise convert using conventional methods.

The CFI for the Thomas Creek mixed conifer watershed provides some insight into the natural processes of fuel accumulation and the effects of fire on species composition. Fuel accumulates naturally in these stands in the absence of fire. When fires do occur they alter this natural process by consuming some of the fuel that has accumulated, and by creating fuel that then becomes available to burn in future fires. The Thomas Creek CFI helps verify that there have been changes in species composition on Thomas Creek since the last major fire in 1893. Aspen has decreased because of the increase in the size and number of shade tolerant mixed conifer species. These shade tolerant species, many of which are easily damaged or killed by fire when they are young, are reproducing under ponderosa pine stands growing on the south slopes. Fire would favor the ponderosa pine component of the stand, and would maintain these small patches of ponderosa pine as a pure type.

Fire history on Thomas Creek seems to indicate that, even with 25-30 years of natural fuel buildup, the few fires that apparently burned over the entire watershed were not of the type that totally destroyed the stand. The presence of old growth trees, present species composition, and range in age classes within the stand bears out this assumption.

SUMMARY

The CFI is a research tool. It is expensive to develop and is probably not a feasible method for the land manager to use in describing fire history for an area. However, if an adequate number of properly distributed specimens can be located, sampled, and accurately dated it is a direct way of reconstructing fire history on relatively small areas. The accuracy and utility of a CFI in ponderosa pine is largely dependent upon precise dating and verification of the fire-scarred material. This means that it is essential to employ established dendrochronological techniques, (e.g., screening for false rings or locally absent rings) in determining dates of fires and fire free intervals. This can be an expensive and time-consuming process, but necessary if the results are to be considered reliable.

A CFI provides an improved understanding of the general climatic factors affecting ignition and spread of historical fires. In ponderosa pine, for example, the closer the fire interval, the more assurance we have that the ignition sources and conditions favoring fire spread occurred simultaneously. In mixed conifer, on the other hand, less frequent fires, and fewer fires covering the area indicate that, although ignition sources were present, critical burning conditions and ignitions occurred simultaneously at less frequent intervals.

The CFI technique may not have application in other forest types. For example, it may not be needed in forested communities having a history of infrequent but destructive fires.

A CFI for a particular area need not be developed all at once. In fact, it may be desirable to locate and collect fire-scarred material from an area over an extended period of time to improve the probability that the best specimens have been collected representing as much of the area as possible. A preliminary CFI can be refined as additional material is located and processed.

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Sonoran Desert Fire Ecology[1]

Garry F. Rogers[2] and Jeff Steele[3]

Abstract.--Repeated observations of permanent plots and transects are used to evaluate adaptive responses of individual species and communities of perennial plants following fires that occurred in 1974. Positive adaptations are common, but are weakly developed. Recovery is taking place, but at a very slow rate. Several decades, at least, will be required for full recovery.

INTRODUCTION

An important objective of fire-ecology research is determination of natural fire frequencies (Vogl 1977). In most vegetation, fires leave dateable evidence such as scars on tree rings (Ahlgren and Ahlgren 1960). In the Sonoran Desert, however, growth is not restricted to a single period, and growth rings are not reliable indicators of age (e.g., Judd et al. 1971). An alternative approach to fire history determination using fire-related adaptations is explored in this report. Separate analyses of the interrelationship of climate, fine fuels, and survival, as well as individual species responses, are being prepared.

Plant species of some vegetation have been shown to have evolved characteristics that favor survival of fire (Gill 1977). In this paper we evaluate post-fire responses of perennial plants, measured for three to five years, to determine whether or not positive adaptations to fire are sufficiently common to suggest an evolutionary history of repeated burning.

Little is known of the ecological role of fire in the deserts of western North America. Most studies of desert fire have actually delt with the semiarid fringe of the desert--the foothill shrubland and woodland of the Great Basin Desert (Wright et al. 1979), the desert grassland of the Southwest (Humphrey 1958), and upper altitude sites in the Chihuahuan Desert (Ahlstrand 1979). One reviewer (Humphrey 1974) regards desert fire to be uncommon, except in areas dominated by native perennial grasses. Studies in the Mojave Desert (Beatley 1966) and the Great Basin Desert (Rogers 1980), however, indicate that sufficient fuel can be supplied by introduced annuals. Similar species of annuals are abundant at times in the Sonoran Desert (Franz 1977).

During recent years fires have occurred throughout the Desert. Arizona Bureau of Land Management (BLM) records show that during the seven-year period 1973-1979, 210 fires burned 36,621 ha in the Arizona Upland and Lower Colorado subdivisions (Shreve 1951) of the Desert. Most fires occur in the Arizona Upland, and it is probable that local topographic and climatic conditions, as well as behavior patterns of prehistoric and modern peoples, could result in much higher frequencies at some locations than at others. The above figures suggest that fire could occur in cycles shorter than the life span of longer-lived Desert species (Shreve 1951), and could be a significant selective force in shaping the life-history traits of individual species.

METHODS

Following fires that occurred in 1974, permanent plots and transects were established in burned, and adjacent unburned, vegetation at two sites in south-central Arizona. One site (Dead Man Wash) is about 45 km north of Phoenix (SE¼ sec. 27, T. 6 N., R. 2 E., Gila and Salt River Meridian), and consists of a 65 ha burn that began at the side of Interstate Highway 17, and was probably man-caused. The other site (Saguaro) is about 50 km east of Phoenix (T. 3 N., R. 8 E., Gila and Salt River Meridian), 105 ha in size, and was also man-caused. Both fires occurred in June.

At each site, two to three chart quadrats (100 to 300 m^2) were established on each of three exposures. Total plot area is 600 m^2 at Dead Man Wash, and 900 m^2 at Saguaro. To supplement plot information, six point-quarter transects (250 to 500 m) were located in predominantly burned vegetation at Dead Man Wash, and four burned

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(500 m) and four unburned (250 m) transects were established at Saguaro. Transects were sampled at 10 m intervals.

Percent kill (proportion of photosynthetic surface scorched or consumed by fire), percent consumption (reduction of total biomass), and resprouting (shoot or leaf growth from roots or scorched stems) were estimated and recorded for all perennial plants during the initial survey. Position of all plants in plots was recorded on graph paper. Identities of mostly consumed plants were determined by comparing remaining stem or root tissues with that of living plants. Errors in identification are most likely for rarer species, and do not greatly influence most results of the study, except the values for species richness and diversity. Presence and resprouting of living plants was recorded during resurveys after four years (51-58 months) at Dead Man Wash, and after three years (34-40 months) at Saguaro.

Data from both surveys are used for mostly qualitative judgements of species and community adaptations to fire (Gill 1977, Mutch 1970). The analysis is limited to perennial plant species, and to the following species traits: 1) bud protection and resprouting, 2) seedling establishment, 3) resistance to fire, and 4) flammability. Bud protection and resprouting are reviewed by Gill (1977). Seedling establishment may have been from seeds surviving fire in the soil, seeds remaining on burned plants, or seeds dispersed from resistant plants within the burn, or from unburned areas.

Resistance to fire, for the purposes of this study, is defined as survival without resprouting or seedling establishment. Survival might thus result from physical resistance to kill and consumption, might be a chance event due to occurrence of a skip (area of unburned vegetation within the larger area of the burn), or might be due to habitat characteristics that decrease fire probability through fuel reduction.

The last trait considered, flammability, is assumed to be closely related to consumption. Whether or not greater consumption is a consequence of greater flammability of one or another species in the way that Mutch (1970) found the litter of fire-prone vegetation to be more easily burned is uncertain. Other characteristics such as canopy height and shape, or interspecific relations with understory species, might also be important.

Community characteristics considered include plant density, species richness (number of species), species diversity (Brillouin index, Pielou 1975), and adaptive characteristics (Grime 1979) typical of early ecological succession.

SPECIES ADAPTATIONS

Resprouting, seedling establishment, and resistance were observed in 13 of 19 species present in all burned plots (Tables 1 and 3). Resprouting was observed in 15 of the original species present in all plots and transects (Tables 1 and 3). Although frequent among the species present, resprouting replaced only seven percent of combined plot and transect numbers, and only two percent of the plants in all burned plots. Resprouting species were more common in Saguaro plots than in Dead Man Wash plots. Most resprouting was by woody shrubs, and least by cacti

Seedling establishment was more abundant than resprouting, and resulted in replacement of 22% of the original plants in all burned plots. Most (82%) seedlings were *Ambrosia deltoidea*. Seedling establishment was greatest at Saguaro, partly because of colonization by two species not recorded during the original survey (*Cassia covesii* and an unidentified species of *Castilleja*), but also because of the greater success of *A. deltoidea* seedlings. At the time of the original survey, seedlings were abundant in the north-facing plots at Dead Man Wash, but few survived until the resurvey. Seedling establishment accounted for 52% of all plants present in burned plots at the time of the resurvey.

Resistance to burning occurred in 9 of the original 19 species in all burned plots. These plants represent 9% of the original number. Most (75%) of the survivors were either *A. deltoidea* or *Larrea tridentata*. Unburned skips were common at both sites, and *A. deltoidea* usually survived by being entirely skipped. In contrast, *L. tridentata* usually survived because of incomplete kill of stems and leaves.

Flammability varied from 95% (*A. deltoidea*, Table 3) to 1% (8 species, Tables 1 and 3). An attempt was made to identify correlation between flammability and survival, but scattergram plots of flammability and resprouting, and other forms of survival, showed no relationship. Most cactus species were only slightly consumed, but *A. deltoidea* was usually 100% consumed unless skipped.

COMMUNITY ADAPTATIONS

Total species densities declined in all burned plots, with greatest decline at Dead Man Wash (Table 2). Transect densities also declined at Dead Man Wash, but no change occurred on Saguaro transects. Resurvey density at Dead Man Wash ranged from 21% to 36% of pre-fire density. At Saguaro, post-fire density ranged from 70% to 100% of pre-fire. This was due both to skips, and to the reproductive success of *Encelia farinosa, A. deltoidea, C. covesii, Castelleja, Acacia constricta, Acacia gregii, and Lycium spp. A. deltoidea* decreased in burned plots at both sites, but increased on transects. *E. farinosa* made the greatest relative increase. Cactus species decreased at Saguaro, and on burned plots at Dead Man Wash. *E. farinosa* appears to qualify, at least in a relative sense, as a ruderial. Its increase while cactus species declined tends to

Table 1.--Dead Man Wash. Data include numbers of plants on both surveys (N1 and N2), numbers of plants resprouting (RS1 and RS2) on each survey, numbers of seedlings and resistant plants, and mean percent kill and consumption.

[1]Species	Burned plots						Burned plots and transects					
	N1	N2	RS1	RS2	Seedlings	Resistant	N1	N2	RS1	RS2	[2]%Kill	[2]%Consump.
mbrosia deltoidea	275	49	0	0	35	14	298	178	5	0	84	73
ereus giganteus	2	1	0	0	0	1	5	1	0	0	65	1
ercidium microphyllum	12	5	0	0	0	5	28	29	3	5	78	1
chinocereus engelmanii	0	1	0	0	1	0	14	2	0	0	97	1
ncelia farinosa	6	3	0	0	3	0	10	27	0	0	79	15
errocactus acanthoides	1	0	0	0	0	0	21	3	1	0	82	1
rameria grayi	2	1	0	1	0	0	28	19	3	12	95	20
arrea tridentata	44	18	2	1	2	15	173	64	9	15	99	23
ycium spp.	2	1	0	0	1	0	9	10	0	2	50	10
ammalaria microcarpa	4	0	0	0	0	0	28	3	0	0	95	1
puntia acanthacarpa	56	3	0	2	0	1	126	69	5	5	89	1
puntia biglovii	0	0	0	0	0	0	52	16	2	0	88	1
lnea tesota	0	0	0	0	0	0	1	3	0	0	100	1
puntia leptocaulis	1	0	0	0	0	0	5	2	0	2	100	15
rosopis juliflora	1	0	0	0	0	0	3	0	2	0	100	73

[1]Species represented by only one or two plants were omitted. They include *Brickellia coulteri*, *astilleja*, and *Ziziphus obtusifolia* all of which were present only on the resurvey, and *Opuntia haecantha* which was present only on the original survey.

[2]The mean values were often accompanied by large standard errors. Reliability increases with N1, but ven with large N1 and small standard error, multiple populations may be present. *A. deltoidea* for example, as almost always 100% consumed unless completely skipped. Rather than indicating that individual plants ere usually only partially consumed, the value of 73% indicates that about 27% of the plants were skipped.

upport Grime's hypothesis that succession in tressful environments will progress from ruderial o tolerant strategies among the species present n the community (Grime 1979). Species richness hanged very little at either site, and diversity ecreases on transects were balanced by increases n plots (Table 2).

Changes in community composition were greatest t Saguaro where seven species disappeared and eight pecies appeared between surveys (Tables 1 and 3). dded species accounted for 9% of the total number of plants recorded on the Saguaro resurvey. Five added species accounted for 29% of the resurvey number of plants in Saguaro plots. Most of the added plants were of two species, *C. covesii* and *Castelleja*, both of which exhibit some ruderial characteristics, including rapid dispersal and growth, and presumably relatively short life spans. Three new species were recorded at Dead Man Wash during the resurvey, and two former species disappeared. Numbers of these plants were quite low, however, and most represented less than one percent of the total pre-fire density.

able 2. Community values for the survey (A) and resurvey (B) for both Saguaro, and Dead Man Wash.

	[1]Density		[2]Richness		[3]Diversity	
	A	B	A	B	A	B
Dead Man Wash						
Plots	68	14	16	17	.44	.56
Transects	11	4	12	10	.78	.71
Saguaro						
Plots	33	23	14	13	.51	.64
Transects	25	25	24	25	.69	.56
Both Sites						
Plots	-	-	19	17	-	-
Combined	-	-	26	31	-	-

[3]Plants per 100 m^2

[2]Number of species.

[3]Evenness, the ratio of the Brillouin index to H(maximum). Natural logs were used.

Recovery of the Dead Man Wash site is proceeding much more slowly than recovery at Saguaro. The reason for this is uncertain. Burning intensity might have been responsible, but this seems unlikely, because kill and consumption were generally higher at Saguaro, and resistance was higher at Dead Man Wash. It seems likely that non-fire factors such as pre- or post-fire drought are responsible for the differences.

CONCLUSIONS AND RESEARCH NEEDS

Although it appears that adaptations to fire are present, they are not strongly developed, and the time for return to pre-fire conditions will be long. At the rate of development observed so far, the Saguaro site would reach original total density after about 5 years, but Dead Man Wash would require 20 years. Original species composition of the sites, assuming this to be a realistic goal (see White 1979), would require many decades to

Table 3.--Saguaro observations of numbers of plants on both surveys (N1 and N2), numbers of plants resprouting (RS1 and RS2) on each survey, numbers of seedlings and resistant plants, and mean kill and consumption percents.

[1]Species	Burned plots N1	N2	RS1	RS2	Seedlings	Resistant	Burned plots and transects N1	N2	RS1	RS2	[2]%Kill	[2]%Consump.
Acacia constricta	12	5	7	3	0	2	19	19	13	6	94	20
Acacia gregii	4	3	3	3	0	0	4	5	3	4	100	47
Ambrosia deltoidea	209	103	0	0	88	15	535	509	0	1	90	90
Argythamnia neomexicanna	0	0	0	0	0	0	0	3	0	0	--	--
Beloperone californica	0	4	0	0	4	0	0	4	0	0	--	--
Brickellia coulteri	0	0	0	0	0	0	4	1	0	0	50	39
Cassia covesii	0	39	0	0	39	0	0	63	0	0	--	--
Calliandra eriophylla	0	0	0	0	0	0	22	12	15	12	100	74
Canotia holocantha	0	0	0	0	0	0	4	1	0	0	0	0
Castilleja	0	10	0	0	10	0	0	16	0	0	--	--
Cercidium microphyllum	4	5	0	0	5	0	24	10	4	1	92	11
Echinocereus engelmanii	2	0	0	0	0	0	6	1	0	0	100	1
Encelia farinosa	0	11	0	0	11	0	18	133	0	1	61	8
Ephedra	11	1	0	0	1	0	52	19	1	5	98	53
Fouquerria splendens	1	0	0	0	0	0	5	1	0	0	100	1
Krameria grayi	9	5	3	3	0	2	86	54	17	29	97	67
Larrea tridentata	9	7	5	0	1	6	76	58	9	6	93	45
Lycium	12	10	7	3	2	5	33	36	9	21	100	51
Mammallaria microcarpa	0	0	0	0	0	0	3	0	0	0	67	1
Opuntia acanthacarpa	23	0	0	0	0	0	65	9	0	0	97	3
Opuntia biglovii	3	0	0	0	0	0	56	18	0	0	98	1
Opuntia leptocaulis	10	1	0	0	0	1	28	4	0	0	96	6
Prosopis juliflora	0	0	0	0	0	0	36	0	0	0	97	34
Simmondsia chinninsis	0	0	0	0	0	0	27	14	4	12	96	42

[1] To save space, species represented by only one or two plants were omitted from this table. They include one unknown species present on the original survey, *Cereus giganteus, Celtis pallida,* and *Olnea tesota,* also present only on the original survey, *Dyssodia porophylloides, Ferrocactus acanthoides, Mullenbergia porteri, Thamnosma montana,* present only on the resurvey, and *Gutierrezia sarothrae* which was present on both surveys.

[2] See the second footnote to Table 1.

develop. Obviously, no community can be adapted to fires that occur more frequently than the period required for the community to replace the majority of its original species in their former proportions. In 1979 Dead Man Wash reburned, again from an ignition point near the highway. The new burn is larger, and contains fewer skips than the 1974 burn. Depending on the relative importance of dispersal of seeds from surrounding, unburned sites, and upon the general success of reproduction, recovery may be slower than after the 1974 fire. Opportunity for soil loss and site degradation (Vogl 1977) is high.

We consider the data made available by this study to be too limited in scope and quantity to yield firm conclusions about natural fire frequency. Too much variability exists between sites to consider the data representative of much of the Desert, and observation time has been too brief for generalizations about recovery rates. Based on the slow recovery rate observed at Dead Man Wash, however, a recommendation for conservative attitudes toward Desert fire management may be appropriate.

In this exploratory analysis a qualitative judgement was made regarding the adaptive characteristics of individual species. Further analysis to define life history traits, including longevity, reproduction, seed sources, phenology, and others, would assist in predicting the progres of succession (Slatyer 1977, Catellino et al. 1979).

The relationship between annual plants and fire requires analysis. At Dead Man Wash the post-fire annual community was diverse, but was generally dominated by introduced species, especially *Erodium cicutarium.* At Saguaro, anothe introduced annual, *Bromus rubens*, appeared dominan Does fire lend a competitive advantage to some species, and, as in the Great Basin Desert, do these species support increased fire frequency (Young and Evans 1973)? Do native annuals alone reach densities great enough to carry fire, or must introduced species be present? Perhaps no fire in the Sonoran Desert has been natural since the introduction and spread of exotic annuals. Both frequency and intensity may have increased.

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Some Questions about Fire Ecology in Southwestern Canyon Woodlands[1]

William H. Moir[2]

Southwestern canyon woodlands, for purposes of this paper, are vegetation types along canyon bottoms for mostly third and fourth order drainages whose streams may be permanent or intermittent. These include habitat types within blue spruce, white fir, ponderosa pine, narrowleaf cottonwood, Arizona cypress, and evergreen oak series (Layser and Schubert 1979). Nearly everywhere the canyon woodlands are subject to fire suppression and intense utilization such as commodity harvests, recreation, or development.

Can studies in fire ecology from one canyon woodland at a certain location be extended or generalized to another location? At present I believe not. Fires in the ecological sense are part of the environment, and we have not yet been able to sufficiently particularize these canyon woodland environments in a classificatory sense. For example, my studies (Moir 1981) in Boot Canyon, Chisos Mountains cannot be very relevant to Rhyolite Canyon, Chiricahua Mountains although the vegetation of both areas is in the Arizona cypress series. A habitat type classification provides a tool for generalization, but is not yet available.

I have often seen dense conifer thickets develop in a wide variety of disturbed upland or slope forests in the Southwest, but these thickets are usually absent, despite fire suppression, along canyon streamside environments. How important, then, is fire in maintenance and succession of canyon vegetation? The Bandolier fire of June, 1977 is instructive. A holocaustic fire that ravaged forests of mesa tops scarcely had any important effect along forests of Frijoles Canyon extending through the burn area. Along mesic canyon bottoms fires may be very local, and perhaps other factors of microsuccession are more critical for determining vegetation composition. To understand the role of fire in canyon woodlands we need information on the autecology and fire tolerances of the many dominant species that comprise the vegetation.

Fire management plans for canyon environments may not require fire history knowledge. Such histories can be irrelevant if intense utilization during the last hundred years has markedly changed the vegetation or if management goals are not directed to any kind of natural maintenance proces However, if Southwestern canyon woodlands are envisioned as natural or scenic areas, refuges, preserves, or wilderness, then the historic role of fire in bringing about or maintaining biotic diversity should be known if possible. In the absence of such knowledge I see little reason why localize prescribed fires cannot be substituted for natural occurring fires. And fires may not be needed at a along third and fourth order drainages where flash floods or other natural channel and fluvial geomorphic processes set the stage for local succession and perpetuate the diversity of these canyon environments.

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Fire History of Western Redcedar/Hemlock Forests in Northern Idaho[1]

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Abstract.--Evidence of fire history over the past few centuries was gathered in two areas (totaling 30,000 acres; 6000 ha) for fire management planning. Findings are some of the first detailed data for western redcedar-hemlock forests. On upland habitat types fires of variable intensities generally occurred at 50-to-150-year intervals, often having a major effect on forest succession. On wet and subalpine habitat types fires were infrequent and generally small.

INTRODUCTION

Prior to the development of modern fire suppression, forest fires, caused largely by lightning, had a major influence in the ecology of Northern Rocky Mountain forests (Leiberg 1898, Larsen 1929, Wellner 1970, Habeck and Mutch 1973). Periodic fires killed varying amounts of trees and undergrowth and consumed duff and litter, allowing shade-intolerant species to perpetuate through seeding or sprouting in what would otherwise have become climax forests (Davis et al. 1980). The history of fires occurring prior to the advent of organized fire suppression in the early 1900's has been studied in many of the major forest types (Arno 1980), but not in the western redcedar (Thuja plicata)-western hemlock (Tsuga heterophylla) potential climax forest types, which are abundant in northern Idaho.

In 1979, L. A. White and D. H. Davis of the Priest Lake Ranger District, Idaho Panhandle National Forests, sought to obtain fire history information to be used as a basis for writing fire management plans for two planning units, Salmo/Priest and Goose Creek, in the redcedar-hemlock forests. In consultation with the senior author, they set up the fire history sampling approach outlined here. Although the approach was not designed for a comprehensive fire history study, the information gathered provides a preliminary overview of fire history in some of the redcedar-hemlock forests.

STUDY AREAS

The Salmo/Priest and Goose Creek planning units are each about 15,000 acres (6000 ha) and are located north and southwest of Priest Lake (fig. 1). Both units are dominated by redcedar

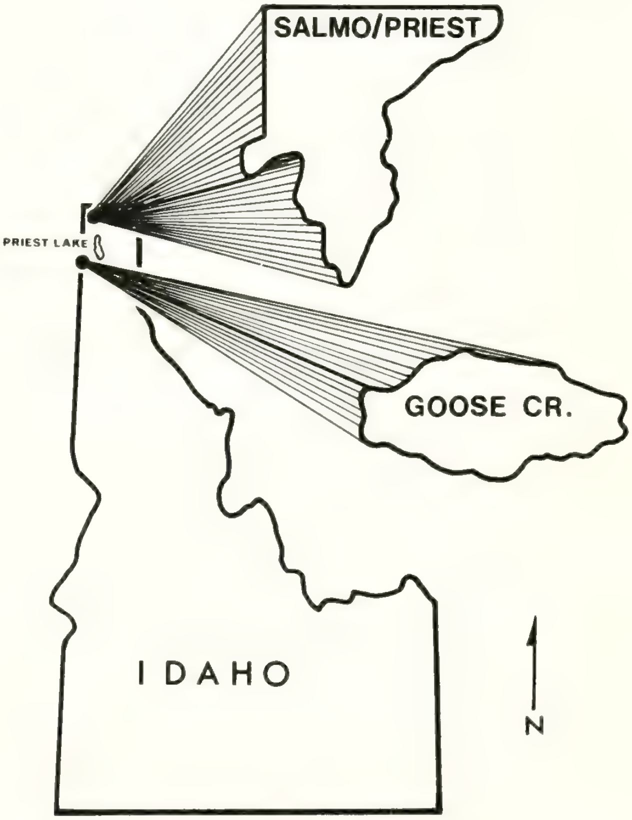

Figure 1.--Location of study areas.

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[1] Paper presented at the Fire History Workshop, University of Arizona, Tucson, October 20-24, 1980.

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and hemlock habitat types (as described by Daubenmire and Daubenmire 1968) on all but the highest elevations. In addition to these shade-tolerant, potential-climax species, however, burned sites support numerous seral trees (shade-intolerant) particularly western white pine (*Pinus monticola*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*). The composition of seral forests varies with site conditions and stand history. Early accounts (Leiberg 1898), 1930's aerial photography, timber type maps, and modern field reconnaissance all suggest that most of the circa 1900 landscape in both planning units was covered with forest stands 100 to 500 years old. Both areas are mountainous and have a cool, inland-maritime climate, with heavy annual precipitation (about 35 to 50 inches in the redcedar-hemlock type). Winters are long and snowy; the short summers have periods of warm, dry weather.

There are some marked differences between the planning units. The Salmo/Priest unit is remote, essentially without roads, development, or timber cutting, and is part of a proposed Wilderness. It has steep, rocky, and rugged terrain with elevations ranging from about 2750 feet (840 m) in the Upper Priest River Valley to well over 6000 feet (1830 m) on major ridges. The fire management plan for this area will be concerned with perpetuating unique wilderness values, including ancient redcedar groves and habitat for the woodland caribou, grizzly bear, and certain bird species considered to be threatened or endangered in the contiguous United States.

In contrast, the Goose Creek unit is less-rugged commercial forest land (mostly between 2500 and 5000 feet (760 to 1520 m) in elevation that has been logged since the early 1920's. Human occupation of the Goose Creek area dates back into the late 1800's and Leiberg (1898) reported that white men (mostly prospectors) set numerous forest fires during that period. The Goose Creek fire management plan will be concerned with protecting and enhancing timber values.

METHODS

In both study areas data on fire history, fuel inventory, timber inventory, habitat types, and soils were collected to provide basic inputs to the fire management plan. Each study area was divided into topographic subunits, small drainages of 150 to 300 acres (60 to 120 ha). In each area nine or ten subunits representative of the terrain and forest conditions were then selected for intensive field sampling. Active cutting units and previously clearcut/burned units in the Goose Creek area were avoided.

Two to three miles of transects were then laid out on a map across elevational gradients in each subunit. Thus, a total of about 25 miles (40 km) of transects were laid out in each of the two study areas.

Field crews gathered fire scar evidence continuously along each transect and good specimens of fire scarred trees were wedge-sectioned with a chainsaw (Arno and Sneck 1977). Inventory plots for dead and down fuel (Brown 1974) were taken at 20 chain (1/4 mile; 402 m) intervals along each transect. A 100-foot-long (30 m) sampling plane was used for inventory of large fuels to minimize error related to variability of the fuel bed. Habitat type (Daubenmire and Daubenmire 1968) and topographic data were recorded at each fuel inventory site.

Two sampling teams (three technicians each) did the sampling over a period of 15 weeks in 1979. Over 100 fuel inventory plots were taken in each study area.

RESULTS AND DISCUSSION

Field Application

To simplify field work crews were directed to select and cross-section a few of the fire-scarred trees as they were encountered along the transects, rather than making an initial reconnaissance and then revisiting and sampling the best specimens (as recommended by Arno and Sneck 1977). The extensive bole rot associated with most old fire-scarred trees (essentially all species) made it difficult for field crews to obtain good quality samples necessary for dating early fires. Many partial cross-section cuts collected were subsequently rejected because of extensive rot or because stems were not sectione deeply enough to identify the year of the fire. We now recommend that in studies of redcedar-hemlock forests many of the trees be felled so that full cross-sections can be taken at the best location along the lower trunk (unnecessary portion of cross sections could be cut off and discarded in the field). Studies might be made in conjunction with logging.

In retrospect, the field crews could have gathered more complete fire scar and stand age-class data if they had been given more training, time, and supervision in the field. Our initial aim of obtaining large numbers of increment borings to identify all age classes of intolerant trees in sample stands was only accomplished in a few revisited stands in the Goose Creek unit. These data were useful for identifying probable fire years based upon vigorous regeneration of shade-intolerant trees such as western larch, Douglas-fir, lodgepole pine (*Pinus contorta* var. *latifolia*), and ponderosa pine (*Pinus ponderosa*). In most stands a thorough investigator could extend the fire history record back to the 1600's using full cross sections of scarred trees and age classes of veteran intolerant trees. A special increment borer at least 24 inches (61 cm) long would be necessary for the latter work.

A confounding problem for field work in redcedar-hemlock forests is that root-rotting fungi, notably Armillaria mellea, scar the bases of trees, sometimes in association with fire scars. However, most root-rot scars are easily differentiated from fire scars. Root-rot scars are associated with root buttresses; whereas fire scars usually are found in hollows between roots on the uphill side of the trunk. Externally, fire scars are usually triangular, while root-rot scars have irregular shapes.

Cross-sections from sample trees were taken to Dr. Arthur Partridge, forest pathologist at the University of Idaho, Moscow, for determination of which scars were caused by pathogens and which by fire. Partridge was able to identify the pathogenic scars by the marked slowdown in radial growth preceding the scar and the evidence of rot associated with the growth rings formed prior to the scar. In most cases, the growth-ring healing pattern associated with pathogen scars was obscure and indefinite in contrast with the relatively clear and simple patterns associated with mechanical scars, including fire scars. Presence of charcoal on the outer bark is often associated with a fire scar as much as 100 years old. Interestingly, we found that although fires had often burned through the bark and cambium of western redcedars and charred areas of the sapwood, the trees continued to live. Similar damage from wildfires usually kills other species of conifers in the Northern Rockies.

Fire History Interpretations

Figure 2 shows the fire scar dates found on individual trees in all subunits.

The "R" symbols in some of the Goose Creek subunits identify age classes of intolerant tree species evidently regenerating within a decade of a given fire year in the stand. This evidence of fire can be viewed as conservative, since field reconnaissance undoubtedly failed to detect and document all evidences of fire. Fire evidence from 1880's and 1890's at Goose Creek probably included some burns caused by European man. But on most subunits the period 1750 to 1900 probably reflects the general lightning fire frequencies, prior to settlement by European man. The frequency of Indian-caused fires in these forests is unknown, but evidently such fires were of minor importance.

As shown in figure 2, one to four fires were detected between 1750 and 1900 in each of the redcedar-hemlock subunits. This suggests average frequencies of about 50 to 150 years for signifi-

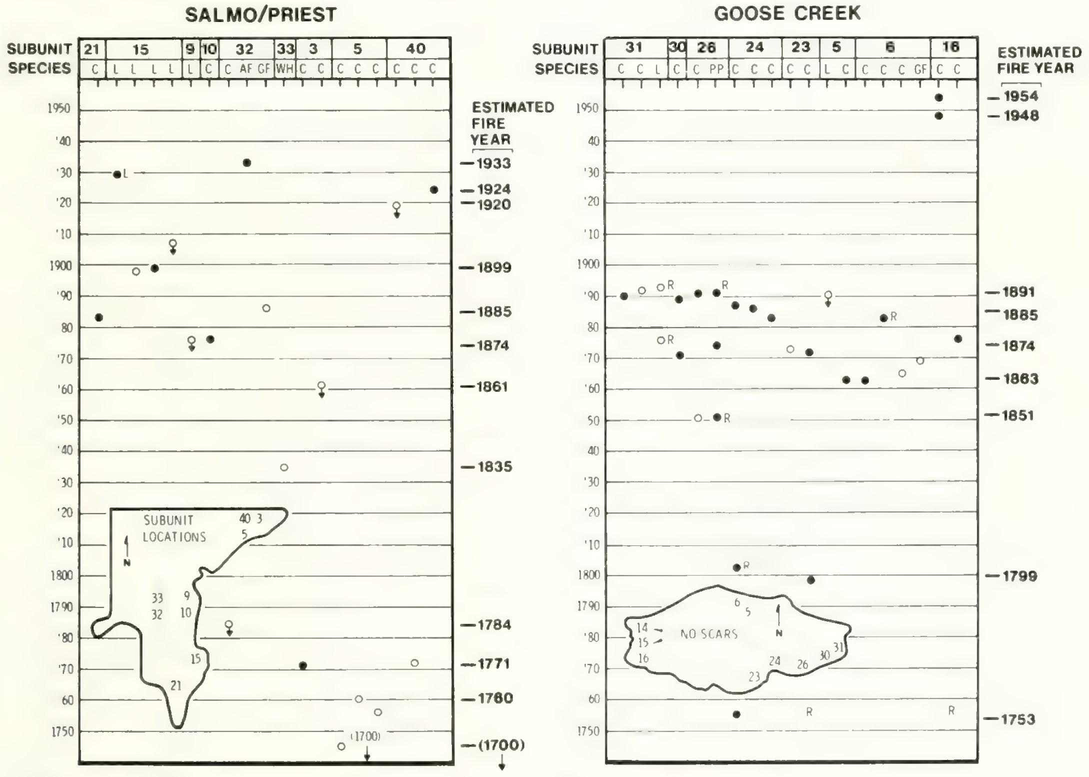

Figure 2.--Master chronology of fire-scar records. Each column represents fire scar records from a different tree. Each dot represents the year of the fire scar. Solid dots indicate clearest ring counts. "R" (regeneration) indicates that an age class of intolerant trees was traced to that fire year. "L" indicates a lightning-strike scar. Tree species are coded as follows:

C = western redcedar
L = western larch
AF = subalpine fir
GF = grand fir
WH = western hemlock
PP = ponderosa pine

cant fires occurring in small stands.

Our reconnaissance data suggest the following interpretations of pre-settlement fire history by habitat types (Daubenmire and Daubenmire 1968). Figure 3 shows the distribution of habitat types in the Salmo/Priest unit.

Upland Redcedar-Hemlock (Tsuga/Pachistima and Thuja/Pachistima h.t.s)

Areas having large expanses of unbroken forest (pre-1900 condition) are represented by the Goose Creek Unit and to a lesser extent by the southern portion of the Salmo/Priest unit. Fire scars and age classes of shade-intolerant trees presumably resulting after fire suggest that significant fires occurred in most subunits once or twice a century since the 1600's. This fire frequency coincides with findings by Marshall (1928) for five stands in the Priest Lake area.

Fires in upland redcedar-hemlock habitats burned under variable intensities, ranging from light ground fires that did little direct damage even to thin-barked overstory trees, to crown fires that covered hundreds of acres in a major run. Overall, fires left a patchy pattern of (1) complete stand replacement, (2) partially killed overstory (resistant species surviving), (3) underburning with little overstory mortality, and (4) unburned forest.

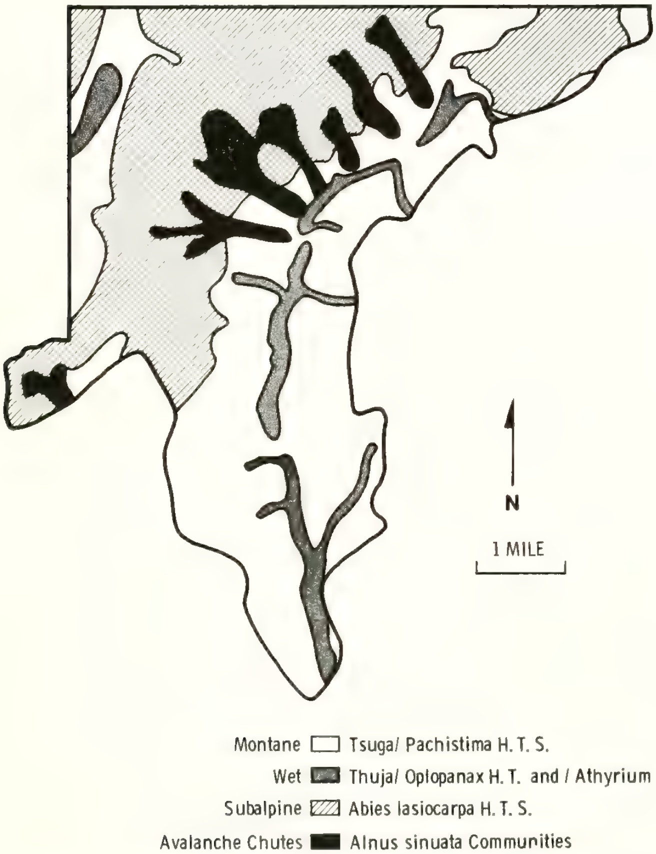
N
1 MILE
Montane ☐ Tsuga/ Pachistima H. T. S.
Wet ▩ Thuja/ Oplopanax H. T. and / Athyrium
Subalpine ▨ Abies lasiocarpa H. T. S.
Avalanche Chutes ■ Alnus sinuata Communities

Figure 3.--Habitat type map of Salmo/Priest unit.

Certain topographic situations were evidently pre-disposed to hot, stand-replacing fires. In the Salmo/Priest unit, field sampling and inspectio of aerial photos and an old fire map identified a mid-slope "thermal belt" that burned hot in the late 1800's. Hayes (1941) documented and described a similar thermal belt on mountainsides south of Priest Lake. These wind-exposed slopes are inherently warmer and drier, and their steep topography would allow pre-heating of live fuels to occur from below. Subunits 5 and 6 at Goose Creek are dense forest habitats on southwest-facing slope exposed to prevailing winds. They were the only subunits on which stands were almost entirely burne and replaced in late 1800's, evidently from a doubl burn in about 1863 and 1885 (fig. 2).

The field data suggest that stands on sheltere north-facing slopes burned less severely, probably because of moist site conditions and less wind exposure. Stands in more rugged terrain (Salmo/Pries unit) apparently burned less often. Natural barrie in these areas would tend to limit fire spread. Th northernmost study subunits (Salmo/Priest 3, 5, and 40) burned less often and apparently less intensely The subunits are dominated by old-growth redcedar-hemlock stands (older than 300 years) divided about every half-mile by large alder-filled snow-avalanch swaths. Wet bottomland forests occur below, and rocky subalpine terrain lies above these redcedar-hemlock stands.

Wet Site Redcedar-Hemlock (Thuja/Oplopanax and Thuja/Athyrium h.t.s)

These poorly drained sites occur along the major streams and in seepage areas. They generally support groves of large (> 500-year-old) western redcedar, except in logged areas. Fires were infrequent other than lightning-strike spot fires and usually had little impact upon these stands. Only rarely a major fire would spread through portions of these communities and cause overstory mortality.

Subalpine Fir Habitat Types (Abies lasiocarpa serie

These sites occur above about 4700 feet (1430 elevation in the Salmo/Priest unit, where they are covered with patchy stands primarily of subalpine fir along with Menziesia shrubs and low growing Xerophyllum. The terrain is very rocky and steep, and forest vegetation forms a mosaic with shrub or herb communities and rockland. The map of 1921 through 1978 fires (fig. 4) shows that lightning fires are frequent. However, field data and distri experience suggest that even without suppression the vast majority of fires would remain small. In nearby areas where high elevation forest is more contiguous on wind-exposed ridges, fires have occasionally spread over sizeable acreages as stand

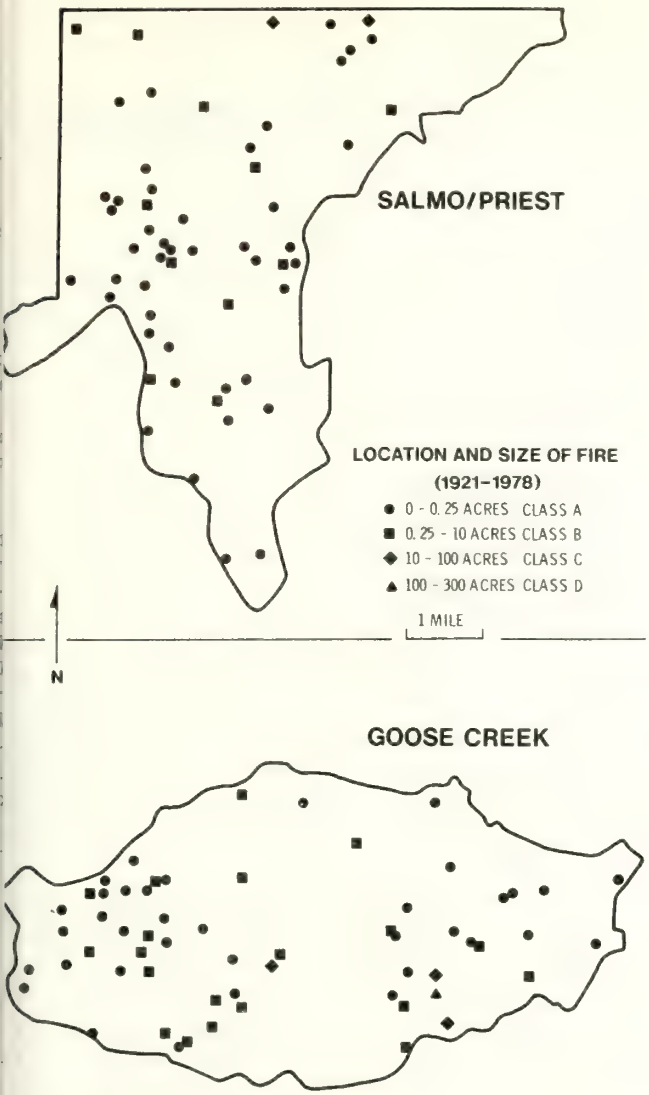

Figure 4.--Location and size of fires 1921 through 1978, from national forest records.

replacement burns.

In the Goose Creek unit subalpine forest is confined to a small area on the highest ridge (subunits 14, 15, and 16, figure 2). These wind-sheltered, east-facing slopes are not rocky and are covered with a dense, moist subalpine fir forest. The stands of oldgrowth, fire-sensitive subalpine fir show very little evidence of fire during the past 250 years.

Management Implications

Table 1 presents the general fire history and vegetative response for both planning units. The characteristically long intervals between fires suggest that half a century of fire suppression in these areas has not yet markedly altered the fire cycles for most natural stands. Similarly, loadings of dead and down fuels have apparently not increased significantly. The inventoried subunits in both study areas had moderate fuel loadings (22 to 40 tons per acre) mostly consisting of large (> 3 inch diameter) fuels.

Logging in these redcedar-hemlock forests creates large amounts of slash or "activity fuels," often totaling 100 tons per acre on clearcut units. Logging also opens the forest canopy and allows the fine fuels to dry and become more hazardous than in uncut stands. (Western redcedar slash is especially flashy and combustible.) Recognizing the hazardous fuels and the need to expose mineral soil to enhance tree regeneration, foresters have developed sophisticated prescribed burning methods coupled with clearcutting 20-to-40 acre blocks of forest.

The fire history of the Goose Creek area suggests that on some sites fire-resistant tree species--western larch, Douglas-fir, and ponderosa pine-- could be managed (perpetuated) via shelterwood or possibly even selection cutting coupled with prescribed underburns for slash disposal and site preparation. Even fire-sensitive white pine, redcedar, grand fir (*Abies grandis*), and western hemlock have withstood light surface wild fires with little damage. This suggests opportunities for hazard reduction and wildlife habitat improvement (i.e., fire-caused resprouting of browse plants) in standing timber. The sensitive trees might, however, develop fungal infections as a result of fire scars.

Fire history has several implications for wilderness management in the Salmo/Priest area. Table 1 suggests that, prior to rigid control, fire was a primary factor in maintaining vegetative diversity. Periodic fires allowed regeneration of western larch, Douglas-fir, paper birch (*Betula papyrifera*), and many shade-intolerant shrub species in what would otherwise have become a climax western hemlock and redcedar forest. The patchy patterns and varying intensities of fire coupled with microsite variability allowed a mosaic of forest communities to develop over the landscape. Elements of the mosaic differed from each other both in composition and in structure (related to time since burning and severity of past fires).

Some of the threatened and endangered wildlife species associated with the Salmo/Priest area are dependent upon specific vegetative communities or combinations of them. Since fire is a chief manipulator of habitat, it may affect the animal needs for better or worse. Habitat needs of each threatened species must be determined along with the means of maintaining those habitat conditions. Fire's future role cannot be taken for granted. For instance, a future wildfire might destroy most of the remaining oldgrowth forest habitat needed by the woodland caribou, whereas a different type of wildfire (or prescribed fire) might help safeguard or improve the same habitat. In the context of wilderness, fire

Table 1. Some fire characteristics and effects by habitat type in the Salmo/Priest and Goose Creek units.

Habitat Types	Topography	General elevations, feet	Dominant trees		Mean fire-free intervals, years	Characteristic fire intensities
			with fire exclusion & no silvicultural treatments	In pre-1900 forests		
Thuja/Athyrium Thuja/Oplopanax	streamside & seepage areas	2500-3500	WRC, WH	WRC, WH	> 200	low
Tsuga/Pachistima Thuja/Pachistima	lower and middle slopes	2500-5000	WH, WRC	WP, WL, DF, WRC, WH, GF, LP, PB, ES, PP	50-150	quite variable
Abies lasiocarpa	upper slopes	4700-7000	AF, ES	WL, LP AF, ES, WBP	> 150	low to medium

Tree species abbreviations:

AF = subalpine fir
DF = Douglas-fir
ES = Engelmann spruce
GF = grand fir
LP = lodgepole pine
PB = paper birch
PP = ponderosa pine
WBP = whitebark pine
WH = western hemlock
WL = western larch
WP = western white pine
WRC = western redcedar

management provides opportunities for maintaining primeval conditions, and the fire management plan is the vehicle for allowing the appropriate use of fire.

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Fire Frequency in Subalpine Forests of Yellowstone National Park[1]

William H. Romme[2]

Abstract.--Dead woody fuels were sampled in 16 upland forest stands representing a chronosequence of forest successional stages. Different fuel components show different temporal patterns, but adequate levels of all components necessary for an intense crown fire are not present simultaneously until stand age 300-400 yr. Therefore, the average interval between successive fires is estimated to be ≥300 yr.

INTRODUCTION

There are two different aspects of fire history that must be distinguished if fire regimes are to be compared in different ecosystems. The first can be called fire incidence, or the number of fires occurring within a study area during a period of time. The second is fire frequency, or the average interval between successive fires on a single site. I determined the incidence of fire on a 73-km^2 subalpine watershed in Yellowstone National Park using fire-scar analysis (Romme 1979). I found evidence of 15 fires since 1600, of which seven were major fires that covered ≥4 ha, destroyed the existing vegetation, and initiated secondary succession. The other eight fires apparently covered very small areas and caused little change in the vegetation. Two large fires in 1739 and 1795 each burned about 25% of the watershed, with the other fires together burning another 10%. These were destructive, stand-replacing burns. Less than 10% of the watershed appears to have burned more than once in the last 350 years, mainly along the boundaries between two burns where the second fire apparently burned a short distance into the area burned earlier before going out. This is indicated by the fact that most fire-scarred trees contain only one scar and are found mainly in clumps that appear to represent the margins of burns. In addition, most forest stands either are dominated by a single age class, representing post-fire establishment, or have an all-aged structure representing 350+ yr without fire.

Because so little of the watershed shows evidence of more than one fire, it was not possible to estimate fire frequency using fire scar analysis alone. Despain and Sellers (1977) hypothesized that fire frequency in this area is controlled by changes in the fuel complex during succession. To test this hypothesis, I sampled dead woody fuels in a chronosequence of stands ranging from early to late successional stages. I then combined these data with the fire incidence data to develop a model for fire frequency in the Yellowstone subalpine ecosystem.

STUDY AREA AND METHODS

The study was conducted on the Little Firehole River watershed located on the Madison Plateau, a large rhyolite lava flow in west-central Yellowstone National Park. Most of the watershed has relatively little topographic relief, with an average elevation of 2500 m. Forests cover 90% of the watershed, with early and middle successional stages dominated by lodgepole pine (Pinus contorta var. latifolia Engelm.). Lodgepole pine also dominates late successional stages on drier sites, but shares dominance with subalpine fir (Abies lasiocarpa (Hook.) Nutt.), Englemann spruce (Picea engelmannii Parry), and whitebark pine (Pinus albicaulis Engelm.) on more mesic sites. Ground cover is generally low and often sparse, dominated by Carex geyeri Boott on dry sites and by Vaccinium scoparium Leiberg on more mesic sites.

I sampled dead woody fuels with the planar intersect method (Brown 1974) in 16 upland stands ranging from age 29 to 550+ years. All stands were located on similar soils and substrata, with most on flat or gently sloping terrain. I counted intersections along 20 transects in each stand, resulting in percent errors (standard error divided by x̄ times 100) of about 10-20 for duff and needle litter, 10-35 for small particles (up to 7.5 cm diameter), and 15-60 for large material (≥7.5 cm). I plotted each fuel component against stand age and looked for apparent temporal patterns. For time periods where an apparent change in a fuel component coincided with events in the development of a forest stand that could be expected to produce such a change, I applied linear regression to determine whether the pattern was statistically significant.

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[1] Paper presented at the Fire History Workshop (Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980).

[2] William H. Romme is Assistant Professor of Natural Science, Eastern Kentucky University, Richmond, Ky. This work was done as part of a doctoral dissertation at the University of Wyoming, Laramie, and was supported by a grant from the University of Wyoming--National Park Service Research center.

RESULTS

Figures 1-3 show temporal patterns in three different fuel categories, each of which has an important influence on fire behavior. Fire ignition and initial spread occur in the needle litter (undecomposed needles, twigs, cone scales, and other small particles on the ground) and 1-hour timelag fuels (1-HR-TL; dead woody pieces ≤0.635 cm diameter) (Brown 1974, Deeming et al. 1977). These small fuels are low in very young stands, but increase to a maximum after 150-200 yr due to litterfall, self-pruning, and suppression mortality in the maturing, even-aged lodgepole pine forest (fig. 1). Small fuels remain constant or decrease slightly in older stands as production of small materials declines and is balanced by decomposition. Even maximum accumulations of fine fuels are relatively low, and probably are not adequate to carry a fast-moving surface fire. With the assistance of the U.S. Forest Service, Northern Forest Fire Laboratory, I applied my fuels data from representative 350-yr-old and 450-yr-old stands to Rothermel's (1972) fire simulation model. Even under high wind and low moisture conditions, the model predicted maximum fire spread rates of 3.0-3.6 m/min and maximum fire intensities of 60-87 kcal/sec/m of fireline, values that are in the same range as those reported for controlled, prescribed fires (Romme 1979).

Potential fire intensity (heat release) and flame height are functions of the total fuel mass (Byram 1959). This is high immediately after a fire, consisting mainly of large, fire-killed stems (fig. 2). The developing even-aged pine forest subsequently contributes primarily small fuels, and decomposition of large fire-killed material results in a net decline in total fuels to a minimum between 70-200 yr. Extensive mortality usually begins to occur in the even-aged pine canopy after 250-300 yr, resulting in an increase in total dead fuels which reaches a peak at ca. 350 yr. In recent uncontrolled fires in Yellowstone Park, D. G. Despain (personal communication) has observed that usually only the partially decomposed ("rotten") wood and the sound material up to about 7.5 cm diameter are actually combusted. However, the larger sound material (1000-HR TL sound fuels) constitutes a major portion of the total fuel mass in stands ≥200 yr old. Therefore, I also examined changes in total fuels excluding the 1000-HR TL sound fuels (i.e., including all rotten material plus sound pieces <7.5 cm diameter), observing the same general pattern except that maximum fuel accumulations occur later, around 450 yr (fig. 2).

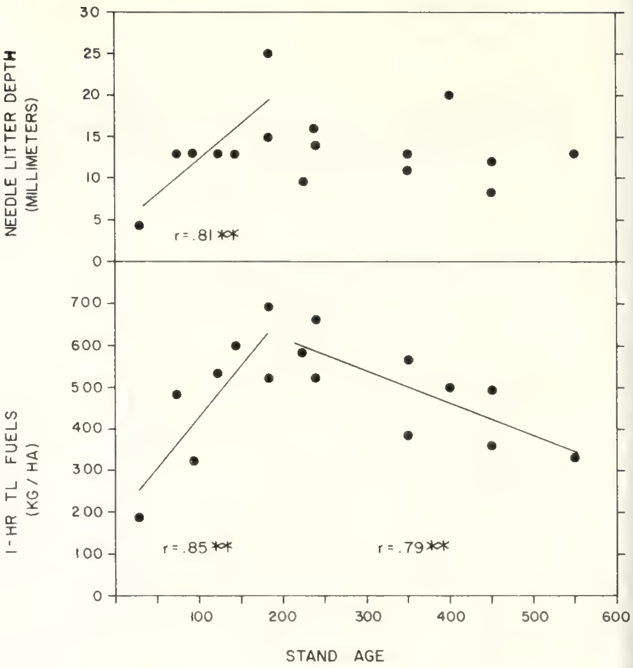

Figure 1.--Temporal changes in small fuels capable of supporting ignition and initial fire spread. The regression line and correlation coefficient are shown for intervals where the slope is significantly non-zero (** = 95% significance level).

An important factor controlling initiation of a crown fire is the vertical continuity between a surface fire and the canopy (Van Wagner 1977). The patterns shown in figure 3 are based on qualitative observations. Vertical continuity is high in very young stands where the small trees have living branches close to the ground. Subsequent self-pruning by maturing lodgepole pine eventually creates a gap between the lowermost branches and the ground. In a 200-yr old pine forest this space may be 3 m or more, and filled only by relatively non-flammable large tree trunks. Around stand age 250-300 yr a well-developed understory usually begins to appear and vertical continuity increases. However, at this time the even-aged pine canopy is usually breaking up, and horizontal continuity appears inadequate for a fire to move through the canopy (although individual crowns may ignite). With maturation of the understory (ca. 400 yr), both vertical and horizontal canopy continuity appear adequate to support a crown fire (fig. 3).

DISCUSSION

The fuels data support Despain and Sellers' (1977) hypothesis that fire frequency in this area is controlled by the slow development during succession of a fuel complex capable of supporting an intense crown fire. Less intense surface fires do occur, but because even the maximum accumulations of fine fuels are comparatively low and because the small needles tend to form a relatively compact litter layer, light surface fires generally spread slowly and cover only small areas. Thus they have a minor impact on overall vegetation structure and dynamics.

The very small quantity of easily ignited fine fuels in early successional stages (fig. 1) makes a second fire unlikely during the first several decades following a destructive crown fire. By stand age 150-200 yr fine fuels have accumulated to maximum levels, but total fuel mass and canopy continuity are by this time very low (figs. 2 and 3). This means that a surface fire is unlikely to generate sufficient heat to ignite the tree crowns, and will probably go out before it burns a large area. Observations of recent uncontrolled fires in Yellowstone Park support this prediction. An intense crown fire burning rapidly through an old-growth spruce-fir forest (≥350 yr old) stopped when it reached a 97-yr old lodgepole pine forest, despite the fact that wind, temperature, and humidity all remained favorable and the pine forest was showered with fire brands (Despain and Sellers 1977).

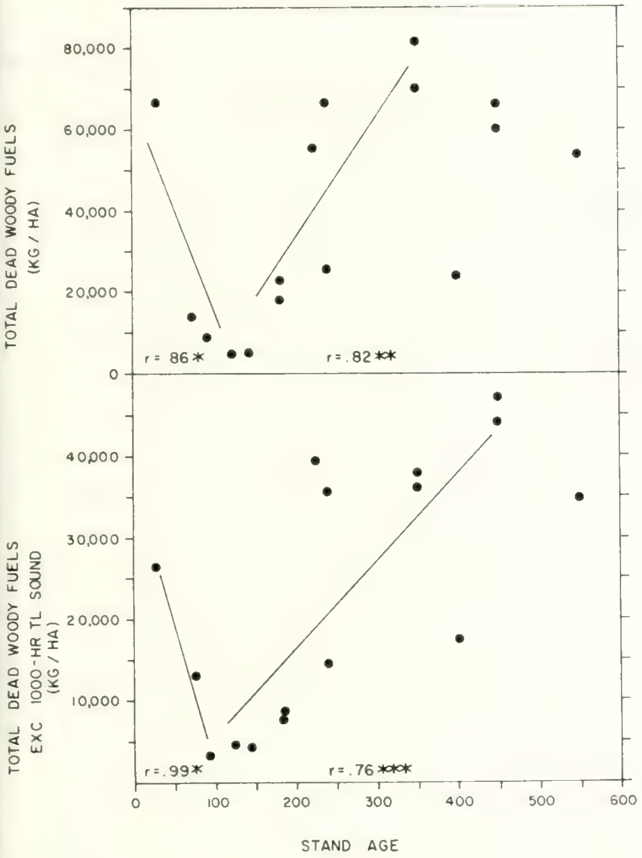

Figure 2.--Temporal changes in total dead woody fuels and in total fuels excluding 1000-HR TL sound fuels. The regression line and correlation coefficient are shown for intervals where the slope is significantly non-zero (*=90% significance level; **=95%; ***=99%).

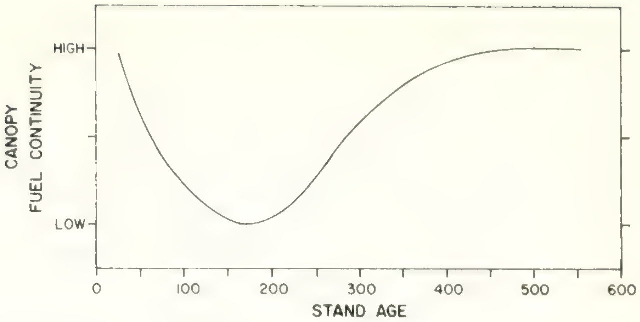

Figure 3.--Qualitative temporal changes in canopy fuel continuity.

Total fuel mass and canopy continuity reach high levels around stand age 250-300 yr and 350-400 yr, respectively (figs. 2 and 3). Fine fuels remain high (fig. 1), having by this time become more heterogeneously distributed with locally large accumulations (Romme 1979). Duff and partially decomposed wood in which a fire can persist during periods of humid or rainy weather (Despain and Sellers 1977) also have reached near maximum levels by this time (Romme 1979). Thus all of the fuel conditions necessary for an intense crown fire are not present simultaneously until stand age 300-400 yr. Once the fuel complex has developed, the actual occurrence of fire is probabilistic, depending on when an ignition source and hot, dry, windy weather occur together (Despain and Sellers 1977). Therefore, I concluded that the usual fire frequency or interval between successive destructive fires on a single site in subalpine forests of Yellowstone Park must be a minimum of 300-400 yr, and it may be much longer.

Fire history studies in subalpine forests of Montana and Alberta have reported fire frequencies (mean fire-return intervals) ranging from 63-153 yr (Arno 1980). These are strikingly different from my estimate of 300-400 yr for fire frequency in subalpine forests of Yellowstone Park. The difference probably results from two factors, the first being the high elevation (2500 m) and comparatively poor growing conditions (average site index 50-60) of my study area. On more productive sites at lower elevations in the Northern Rockies, tree growth and fuel accumulation probably occur more rapidly between fires, making more frequent fires possible (Arno 1980). The mountain pine beetle, which hastens fuel accumulation, is also generally more abundant at lower elevations. Bevins et al. (1977), using data from a large area in southwestern Montana, found patterns of fuel accumulation in relation to stand age that are very similar to the patterns in figures 1-3, except that major changes in fuel quantities generally occur 50-100 yr earlier in Montana. The second factor is related to the types of fires being considered. My estimate for Yellowstone applies only to the frequency of destructive, stand-replacing burns; whereas the estimates from the Northern Rockies include a range of fires from low intensity, non-stand-replacing burns through high intensity, stand-replacing burns. Apparently the low intensity fires are more common and cover larger areas in the Northern Rockies, where they consume a portion of the accumulated fuel and delay the occurrence of high intensity, destructive fires (Arno 1980).

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Interpreting Fire History in Jasper National Park, Alberta[1]

Gerald F. Tande[2]

Abstract.--Fire history in coniferous forests (1665-1975) was related to cultural history and past climate. Fire periodicity increased significantly after European man arrived in the early 1800's. In contrast, extent of fires was not consistently correlated with cultural history periods, but was correlated with climate. The fire regime must be cautiously interpreted in relation to these factors.

INTRODUCTION

In the past decade, historic fire regimes for arious coniferous forest ecosystems have been escribed using dendrochronological techniques. uch studies were lacking for the Canadian Rocky ountains until 1977 when this study was completed.

The 43,200 ha study area occupies the Athabasca, Maligne, and Miette River valleys which converge near asper townsite, Jasper National Park, Alberta. omplex topographic relief varies from gentle sloping erraces and flat valley bottoms to cliffs and ridges f exposed bedrock.

The area represents the extreme northern limit f the eastern Rocky Mountain montane forest zone. alley bottoms and slopes are predominantly covered y lodgepole pine *(Pinus contorta)*. Douglas-fir *Pseudotsuga menziesii)*, white spruce *(Picea glauca)*, rembling aspen *(Populus tremuloides)*, and balsam oplar *(P. balsamifera)* also occur over a moisture nd elevational gradient. Grassland-savanna areas re frequently found in valley bottoms. Higher elevaions are dominated by englemann spruce and subalpine ir *(Picea engelmannii-Abies lasiocarpa)* forest. Lodgepole pine, however, occurs where portions of hese forests have been burned by past fires.

The study area lies in a marked rain shadow of the continental divide. As a result, seasonal total precipitation is lower, and mean daily temperature for May-September warmer than any other part of west-central Alberta. Jasper lies in an area of low lightning frequency, experiencing less than two lightning fires per million hectares per year.

METHODS

Airphoto interpretation was used to distinguish vegetation pattern across the study area. A total of 889 stands were visited and sampled. Vegetation was systematically studied enroute to and within each stand, and fire margins were located and characterized. Changes in species composition, size classes of trees, and remnant stands that had survived previous fires were recorded. Fire scars were collected to document fire dates and increment cores were taken from post-fire trees.

Age data were used to determine areal extent of past fires. The scar dates were used to establish a fire chronology and verify dates of origin for forest stands wherever possible. The fire chronology was based upon 664 fire scars from 435 trees. Airphoto interpretation, field notes, and stand origin dates from 3,388 lodgepole pine and 110 Douglas-fir were verified with the fire-scar record. All of this information was used to construct a stand origin map depicting different forest stands and the fire or fires from which elements of the stand originated. A series of fire year maps was prepared from the stand origin map and field evidence. Details of these techniques are discussed by Tande (1979).

Historical sources from regional museums and archives were reviewed to reconstruct historical geography, check for fire occurrences, and verify fire dates if possible. Incomplete fire statistics for the Park were examined but all fire records from 1907-1968 have been lost or destroyed. As a consequence, the periodicity and pattern of past fires must be based on the fire-scar record and stand origin data.

RESULTS AND DISCUSSION

Fire Regime

The fire history chronology for the 311-year period, 1665-1975, encompassed 72 fires (table 1). Lodgepole pine yielded scar dates back to 1758, and stand origin dates to 1714. Douglas-fir was used to extend the chronology back to 1665. No variations in dates due to false or missing rings were encountered for lodgepole pine. However, Douglas-fir dates varied by ±2 years because of insect damage, resin deposits, and charring by subsequent fires.

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[1] Paper presented at the Fire History Workshop. Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980].

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The fire scars show that there was a fire in the area every year between 1894 and 1908 (table 1). Fires occurred at 1-9 year intervals from 1837-1971. Intervals were much wider from 1665-1834, varying from 1-36 years. There was a notable decline in the portion of area burned after 1908, corresponding with effective fire suppression in 1913.

There was a fire in the area on an average of once every 4.4 years from 1665-1975. Before effective fire suppression, 46 fires occurred with a mean fire return interval (MFRI) of 5.5 years. Those covering more than 500 ha had a MFRI of 13 ranging from 1-27 years. Fires covering more than 50 percent of the valleys had a MFRI of 65.5 ranging from 42-89 years. Thus, the area experienced recurring fires of widely differing size, with larger fires occurring at much longer intervals.

The stand origin map depicts the present vegetation of the area in terms of its past fire history. It and individual fire year maps have previously been published (Tande 1979). Interactions of fire periodicity, intensity, and areal extent were evident in the diverse pattern of stand age structures. These patterns and field evidence were used to infer the corresponding fire intensities (Tande 1979).

The Jasper fire regime was characterized by frequent and extensive low- to medium-intensity fires and occasional, medium- to high-intensity fires for the period 1665-1913. This fire disturbance regime was responsible for a landscape in all stages of secondary succession. Four major types of vegetation pattern are described in Tande (1979).

Influence of Man on Fire Regime

Archaeological evidence indicates that man has been in the Jasper region for at least 10,000 years. The Athabasca and Miette River valleys have been major corridors through the mountains for all of recorded history and were probably used earlier. European man used these valleys since ca. 1800. Because man has been an integral part of the Jasper environment, his role must be examined when interpreting fire history. One could assume that with greater numbers of people there would be a corresponding increase in fire periodicity. During the period of record, we must consider not only this possible increase in human activity, but also the type of human activity. This is because native use of the area overlapped with use by European man. These cultural distinctions may have resulted in different uses of fire.

The human history of the Jasper Park region has been divided into six major periods (Tande 1977) as follows: The Pre-European Period (ca. 10,000 B.P.-

Table 1. Fire scar dates, intervals between fires, and areal extent of individual fires in Jasper National Park, Alta.

Date of fire	Interval since last fire, years	Major fires[b]	Interval since last major fire, years	Portion of study area burned, %	Known area of burn, km²	No. fire s four
1971	6			0.03	0.22	1
1965	1					1
1964	5					1
1959	3					1
1956	2					1
1954	2					1
1952	1					1
1951	1					2
1950	4					1
1946	2			0.02	0.09	1
1944	1					1
1943	4					1
1941	1					4
1940	1					1
1939	3					1
1936	2			0.2	0.68	5
1934	1					1
1933	1					2
1932	3					1
1929	1					1
1928	3					2
1925	2					1
1923	5					1
1918	3					1
1915	1					9
1914	4					2
1910	2					8
1908	1	**	2	1.4	5.98	17
1907	1			0.8	3.52	7
1906	1	**	1	8.1	34.19	34
1905	1	**	1	4.8	20.47	36
1904	1	**	15	1.2	5.29	4
1903	1					2
1902	1			0.4	1.71	3
1901	1			0.3	1.17	4
1900	1			0.2	0.85	2
1899	1					1
1898	1			0.1	0.21	4
1897	1			0.1	0.21	2
1896	1			0.3	1.07	3
1895	1			0.1	0.32	3
1894	2			0.1	0.16	1
1892	3					1
1889	1	**	1	78.5	338.39	287
1888	5	**	4	2.7	11.64	16
1884	1	**	1	1.8	7.90	7
1883	3	**	3	2.0	8.64	13
1880	2	**	11	1.2	5.29	5
1878	2					2
1876	7					1
1869	6	**	6	1.9	8.00	7
1863	2	**	2	5.5	23.59	12
1861	3	**	3	1.8	7.79	2
1858	7	**	11	8.7	37.68	13
1851	4			0.1	0.32	3
1847	1	**	1	52.3	225.45	34
1846	9	**	9	5.3	22.74	18
1837	3	**	3	18.5	79.74	14
1834	13	**	27	5.6	24.23	13
1821	10			0.2	0.64	2
1811	1					1
1810	3					1
1807	10	**	10	8.2	35.44	3
1797	17	**	17	6.7	28.71	10
1780	9	**	22	2.4	10.14	2
1771[c]	13			0.4	1.49	1
1758	21	**	21	50.9	219.42	6
1737[c]	10	**	10	15.5	67.04	2
1727[c]	13	**	13	12.8	55.08	2
1714[c]	36	**		2.8	11.96	1
1678[c]	13	?		0.8	2.92	1
1665[c]		?		0.9	4.05	1
						Total 664

All scar dates are from lodgepole pine unless otherwise noted.

[b] A major fire constitutes a fire burning more than 500 ha (1.2% of the total area).

[c] Tentative dates based on two Douglas fir fire sections. Fire dates of Douglas fir have been found to va by ± 2 years when compared to known dates of the area they were collected in.

ca. 1800) was a period of low population density. Small nomadic groups of forest Indians passed through the area but were never permanent residents, owing to harsh mountain environments and sparse game populations.

The Fur Trade Period (ca. 1800-ca. 1830) was an exploration period of major mountain passes as early as 1770-1802. Trading posts north of the study area were sporadically occupied until 1884, and small populations of Indians resided in the valley near these posts. The entire Jasper region was probably penetrated by trappers by 1825.

Trappers, travellers, and explorers passed through the area especially during the first 35 years of the Presettlement Period (ca. 1830-1892). Accounts suggest that there were few, if any, area inhabitants. Continuous local activity was probably less pronounced than during the fur trade.

Approximately 100 natives and homesteaders lived in the area during the Settlement Period (1892-1910). All but one were evicted by 1910. The area was also visited by mountain climbers and scientists, but activity was generally low.

Jasper National Park was established in 1907, before the Railroad Period (1909-1912). Fire control followed rapidly when the railroad company recognized the tourism potential of the Park. The Park had its first three wardens in 1909 as railroad fire hazards and game poaching increased.

In 1913, the railroad began bringing people to Jasper for scenery and recreation, thus beginning the Park Period (1913 to present). The study area has had effective fire control since 1913 because the valley is a major transportation corridor as well as recreation center.

The total number of fires by historical periods increased from past to present, with the exception of the Railroad Period when number of fires was less (table 2). Fire periodicity shortened from 15.1 years in the Pre-European Period to 1.2 years during the Settlement Period. This increase in fire may be related to increased human activity with time, however, it is partially a result of erasure of older fire sign by subsequent fires. With the establishment of active fire suppression in the Park Period, average fire frequency decreased to one fire every 2.4 years. Since 1908, there have been no major fires and only 0.004% of the area has been burned per year.

The only fire year recorded in the Railroad Period was 1910. Scattered locations of fire scars suggests a number of fires within the year but only a negligible area burned (table 2). Locations are in close proximity to the railroad (Tande 1979), and therefore may have been caused by man. The long MFRI for this period is attributed to wet weather during fire seasons, better patrols on railroad right-of-ways, and mandatory spark arrestors on locomotives (Tande 1979). These results contrast with other major corridors through the Rockies where fire frequency and extent increased during railroad periods.

The Settlement Period had the shortest MFRI with a fire occurring every 1.2 years. The total area burned per year, however, was only 0.99%, whereas 3.0% burned per year in the previous period. While most fires were small, three fires covered 15.5% of the total area. This increase in frequency could have been caused by increasing numbers of people. However, the increase is not necessarily related to an increase in extent of fires. In fact, periodicity appears negatively correlated with extent. This would happen if climate were not conducive to large fires during the period. It could also result partly from suppression efforts and prescribed use of fire by settlers.

Fires of the Presettlement Period account for most of the area burned from 1665-1975. Three percent burned per year, and 13 of the 16 fires were of major extent. The MFRI was 3.9 years, or three times that of the Settlement Period. This decrease in frequency is particularly interesting because there were more people through the area compared to the Settlement Period. In comparing these two periods, we again see that there may not be a causal relationship between fire frequency and extent. If there were, we would expect reduced frequency to have resulted in a reduction of total fire extent.

Table 2. Mean fire return intervals (MFRI) and burned areas for cultural history periods.

ultural Period	Length of record	Number of fires	MFRI (range)	Number of major fires*	MFRI for major fires* (range)	Area covered by major fires* (%)	Forest burned per year (%)
otal Period (1665-1975)	311	72	4.3 (1-36)	24	13.0 (1-2)	300.5	0.98
ark Period (1913-1975)	63	26	2.4 (1-6)	--	---	--	0.004
ailroad Period (1909-1912)	4	1	4.0 ---	--	---	--	--
ettlement Period (1892-1910)	19	16	1.2 (1-2)	3	6.3 (1-2)	15.5	0.99
resettlement Period (1830-1892)	63	16	3.9 (1-9)	13	4.8 (1-11)	185.8	3.00
ur Trade Period (1800-1830)	31	4	7.8 (1-10)	1	31.0	8.2	0.28
re-European Period (1665-1800)	136	9	15.1 (9-36)	6	22.7 (10-22)	91.1	0.69

Fires burning more than 500 ha are termed "major fires" in this study.

As expected, the decrease of activity in the Fur Trade Period resulted in a decrease in fire frequency. In fact, the MFRI was almost double that of the Presettlement Period. Only four fires are recorded, of which one major fire is responsible for most of the total area burned. The cooler, wetter climate of this period apparently inhibited fire ignition, or large extent of fires (Tande 1978). In addition, trappers may have been more careful with fire due in part to a Hudson Bay Company's edict on this subject.

The total area burned per year in the Pre-European Period was more than double that in the Fur Trade Period, although MFRI also doubled. This strongly suggests that man's later influx may have influenced periodicity, but did not necessarily affect total area burned. In fact, the larger extent of fires before 1800 may indicate another factor which governs areal extent and periodicity.

In contrast with fire periodicity, the extent of area burned per year in Jasper fluctuated erratically and is not consistently correlated with human-use patterns. This is especially true of the larger area burned per year before the arrival of the white man in the early 1800's. Other workers have obtained estimates of forest burned per year after 1830 for different regions in the Canadian Rockies. These figures indicate that frequency and areal extent of forest fires were similar throughout the region, even though the areas did not experience equivalent human-use patterns (Tande 1977). Based on these observations, climate may have been the principal factor which controlled the extent of past fires.

Climate

To test the influence of climate, environmental indicators were sought for periods which might correpond to fire years. Since no precipitation records exist for Jasper before 1918, the below-average growth rates of trees in the area were used as indicators of major drought years (Tande 1978).

When all fires between 1700-1913 were plotted against below-mean precipitation periods, 76% of the fires and 92% of the total area burned were accounted for. The 1758, 1847, and 1889 fires occurred during pronounced droughts and accounted for 61% of the total area burned. Only 8% of the area was covered by fires during above-mean precipitation periods. Since the probability of fire is greater during such below-mean precipitation periods, climate was the major environmental factor controlling the extent of past forest fires.

CONCLUSIONS

Man and lightning are only sources of ignition, and whether a forest burns or not is dependent on vegetation and climatic conditions at the time of ignition (Tande 1978). Regardless of ignition source, a climatic change can result in an increase or a decrease in fire extent which will be reflected in annual burn figures. The problem, however, is that the number of fires and their extent may also be affected when man is present. In this study, it appears that European man has increased fire periodicity in certain time periods since 1800, while having variable effect on fire extent. Data from historical sources, fire history, and climate strongly suggest that native man's impact was negligible. These factors affect the fire history chronology and hence our interpretation of fire regime.

Although the tree-ring record shows that fire has been an important environmental factor shaping the vegetation of Jasper from 1665-1913, caution must be exerted in interpreting this fire history as a "natural fire regime." European man has been part of the Jasper environment for over half the tree-ring record of fire. This means that we must rely more on the portion of the record before 1800 to interpret a more "natural role of fire." Unfortunately, this portion of the fire history data has suffered the greatest loss of information over time due to erasure by subsequent fires.

For these Pre-European fires (1665-1800) there is insufficient evidence to characterize the fire severities. Thus we cannot compare a fire regime of this period with that which has been determined for the total period of record 1665-1913. Without a comparison we cannot determine how representative the fire regime is after the early 1800's.

Even though we may never know the actual sources of historic fires, we must attempt to refine our understanding of past fires in Jasper National Park. Management decisions depend on the best possible interpretation of such information. It will be important to determine the incidence and extent of fire before 1665 to test whether the tree-ring record of historic fires is representative of the Jasper ecosystem.

I recommend that a paleoecological investigation be carried out to document the frequency of fire over a longer time period and allow comparison with the more recent tree-ring record. Likewise, further anthropological and historical geography studies would clarify man's use of fire in the Jasper region. These data are needed before the tree-ring record can be accepted or rejected as the typical forest fire situation in the study area.

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Indian Fires in the Pre-Settlement Forests of Western Montana[1]

Stephen W. Barrett[2]

Abstract.--Presents preliminary results of a two-year study examining the pattern of Indian fires in western Montana's lower elevation forests. Interviews and historic journals were used to reconstruct the characteristics of aboriginal burning. Fire scar data from paired stands indicate substantial differences in fire frequency between Indian habitation zones and remote areas before 1860. Fire frequency between the paired stands varied during the settlement period (1861-1910), and fire frequency has been markedly reduced in most stands since the advent of organized fire suppression after 1910.

INTRODUCTION

The influence of Indian-caused fires on the ecology of Northern Rocky Mountain forests has not been investigated, even though such fires are known to have occurred. Schaeffer (1940), Malouf (1969), and Arno (1976) all cite individuals who believed Indian fires occurred before the start of European settlement around 1860. Arno's (1976) fire history study in the Bitterroot Valley documented fires back to about the year 1500. He speculated that Indian fires may have been a factor in several stands having notably high fire frequencies. Mehringer et al. (1977) examined pollen cores from Lost Trail Pass Bog at the head of the Bitterroot Valley. A 12,000-year sample showed a marked increase in airborne charcoal deposits during the past 2,000 years, suggesting a substantial increase in low-intensity fires. However, the mesic climate of that period was not conducive to increased lightning fire occurrence and the researchers considered Indian fires a plausible explanation for the phenomenon.

In 1979 I began a two-year study of Indian fire practices in western Montana. The objective was to determine the ecological effects of Indian-caused fires on Ponderosa pine (Pinus ponderosa)/Douglas-fir (Pseudotsuga menziesii) forests west of the Continental Divide. This report describes the pattern of Indian fires in the region; final results and conclusions are expected by June 1981.

INTERVIEWS AND JOURNALS

Human habitation of present-day western Montana began at least 6,000 years ago (Malouf 1969). The Flatheads and Pend d'Oreilles (collectively known as Salish), and Kootenais were the principal tribes occupying the area when the Lewis and Clark Expedition entered the region in 1805.

The main objective of the 1979 field season was to determine whether Indians set purposeful or unplanned fires in western Montana before intensive settlement by Europeans after about 1860. I also attempted to document details of Indian burning, such as reasons for fire use, seasons of burning, periodicities, and locations and vegetative types where fires occurred. I interviewed descendents of Indians and homesteaders and researched historic journals. Of 60 persons interviewed 24 said Indians purposely set fires, 7 denied this, and 29 did not know. For example, one informant said that in the 1880s his father saw Flatheads burning meadows every few years when they passed through the Ninemile Valley west of Missoula. Journals also often identify Indian fire locations and, as figure 1 indicates, Indian-caused fires were both geographically and temporally widespread.

Most Indian fires occurred in valley grasslands and lower-elevation forests dominated by ponderosa pine, Douglas-fir, or western larch (Larix occidentalis). Ignitions such as signal fires also occurred in high-elevation forests but were relatively rare. According to informants, Salish and Kootenais purposely set fires during fall and spring when climate and fuel conditions are often conducive to low-intensity fires. Journals indicate

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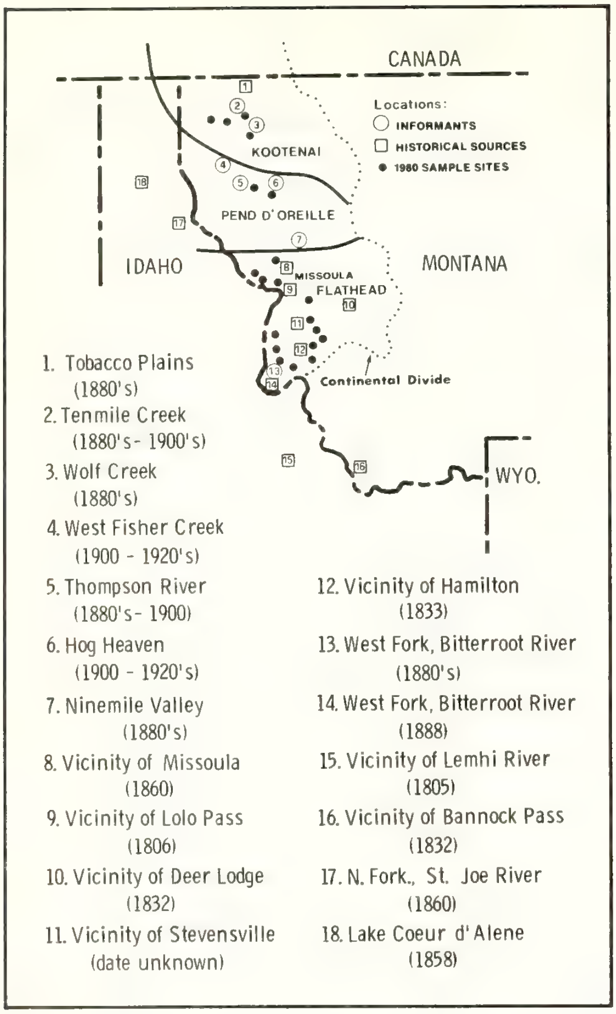
CANADA
Locations:
○ INFORMANTS
☐ HISTORICAL SOURCES
● 1980 SAMPLE SITES
KOOTENAI
PEND D'OREILLE
IDAHO
MONTANA
MISSOULA
FLATHEAD
Continental Divide
WYO.
1. Tobacco Plains (1880's)
2. Tenmile Creek (1880's - 1900's)
3. Wolf Creek (1880's)
4. West Fisher Creek (1900 - 1920's)
5. Thompson River (1880's - 1900)
6. Hog Heaven (1900 - 1920's)
7. Ninemile Valley (1880's)
8. Vicinity of Missoula (1860)
9. Vicinity of Lolo Pass (1806)
10. Vicinity of Deer Lodge (1832)
11. Vicinity of Stevensville (date unknown)
12. Vicinity of Hamilton (1833)
13. West Fork, Bitterroot River (1880's)
14. West Fork, Bitterroot River (1888)
15. Vicinity of Lemhi River (1805)
16. Vicinity of Bannock Pass (1832)
17. N. Fork., St. Joe River (1860)
18. Lake Coeur d'Alene (1858)

Figure 1.--Known Salish or Kootenai ignitions in the region (ca. 1805-1920) and 1980 sample stand distribution. Solid lines indicate tribal distributions as of 1855 (after: Malouf 1974).

Indians also set fires during summer months, usually by accident (Mullan 1861; Phillips 1940; Schaeffer 1940). Summer fires might well have burned hot enough to kill overstory trees.

Although some persons may have been aware of only one purpose for burning, most intentional fires probably were set to achieve more than one objective simultaneously. For example, several informants said fires were commonly set to "burn out the old, dense underbrush" and stimulate new growth of big game browse. Some said Indians set these fires to enhance berry production or to aid food gathering and travel. Others claimed the Indians burned understories to protect the forest from crown fires by reducing fuel accumulations. These statements and certain journals (Jacquette 1888; Elrod 1906) suggest Indians knew such fires could produce many ecological benefits. It is possible, however, that some informants' perceptions of Indian fire practices were inaccurate. For example, several people said the Salish and Kootenais set fires in order to maintain open, healthy timber stands. Although such stands may have resulted from frequent man-caused and lightning fires, it does not seem likely Indians set fires to benefit the forest. Similarly, one Salish informant said her mother-in-law and others burned lichens that hang from trees to reduce the threat of wildfires spreading to the forest canopy. If this actually happened, such burning probably was not widespread. Some persons portray the Salish and Kootenais as having been "wise ecologists" but this was not always the case. Journals show Indians also caused careless, destructive fires (Phillips 1940; Johnson 1969; Malouf 1969).

Six informants said the Salish and Kootenais burned to improve forage for horses. The tribes acquired large herds after about 1730 (Roe 1955). Twelve persons said Indians used fire in various ways to improve hunting. Fires were set to favor big game browse, in addition to being used for drives and surrounds. In the winter of 1858 Father Pierre DeSmet wrote about Salish Indians near Lake Coeur d'Alene in present-day northern Idaho:

> On both ends of their line they light fires, some distance apart... The frightened deer rush to right and left to escape. As soon as they smell the smoke of fires, they turn and run back. Having the fires on both sides of them and the hunters in the rear, they dash toward the lake, ... they jump into the water as the only refuge left for them ... (the hunters) let the animals get away from the shore, then pursue them in their light bark canoes and kill them without trouble or danger. (Chittendon and Richardson 1969:1021-22)

Apparently most purposeful fires were set to improve horse grazing (after 1730) or hunting. These and careless fires probably affected the most acres and thus, are of most interest to ecologists.

Six informants said Indians burned forest understories to encourage food plants, mostly berry-producing species. A Kootenai informant claimed fire also was used to protect medicine plants. His father was a shaman ("medicine man") and told him small ground fires were set to burn unwanted vegetation and to fireproof the area from wildfires Similarly, six people said Indians often set small fires in and around campsites to clear the tall grasses, weeds, and brush that could conceal enemies Campsites also were cleared for protection from natural fires or enemy-caused fires. Other studies (Stewart 1954; Lewis 1977) have found that Indians in other regions practiced such burning to create supplies of small firewood or to eliminate insects. Small strip fires may not have affected forest ecosystems to any considerable degree.

The Salish and Kootenais often set fires for communication. In August 1805, members of the Lewis and Clark Expedition saw large signal fires near the Lemhi River in north-central Idaho:

> This day warm and Sultry, Prairies or open Valies on fire in Several Places. The

> countrey is set on fire for the purpose of collecting the different bands (of Pend d'Oreille), and a band of Flat Heads to go to the Missouri (River) where they intend passing the winter near the Buffalow ... (Thwaites 1969:49)

Salish and Kootenai signal fires were built large so as to be seen from afar. Small campfires with sophisticated blanket-signaling are a myth. Thus, communication fires had considerable potential to to influence forest ecosystems.

One Salish informant said Indians sometimes cleared overgrown trails with fire. Several historic sources corroborate this statement (Ayers 1899; Johnson 1969). Such fires could affect forest development because they apparently were set in dense vegetation at lower elevations.

Journals indicate Indians often caused accidental fires in the region, although informants did not verify it. For example, in 1832 a trapper named Ferris saw the following incident near present-day Deer Lodge, Montana:

> ...I discovered the burrow of a species of beautiful small spotted fox, and ... sent a (Flathead) Indian boy to camp for a brand of fire... The careless boy scattered a few sparks in the prairie, which, the grass almost instantly igniting, was soon wrapped in a mantle of flame. A light breeze from the south carried it with great rapidity down the valley, sweeping everything before it, and filling the air with black clouds of smoke. ... It however occasioned us no inconsiderable degree of uneasiness as we were now on the borders of the Blackfoot country, and had frequently seen traces of small (war) parties, (which) might be collected by the smoke ... Clouds of smoke were observed on the following day curling up from the summit of a mountain ... probably raised by the Blackfeet to gather their scattered bands, though the truth was never more clearly ascertained ... (Phillips 1940:106-07)

In contrast to findings in other studies (Reynolds 1959; Lewis 1977), tribes in western Montana apparently did not set purposeful fires with much sophistication. Except when used to clear campsites, or during dry weather, fires probably were set arbitrarily and unsystematically. Historical references indicate haphazard ignitions were characteristic (Ayers 1899; Phillips 1940; Johnson 1969; Malouf 1969). Most informants said intentional fires were set and allowed to burn freely because the Indians often were passing through or leaving an area and did not intend to return for long periods. Informants could not give detailed information on fire periodicities, further indicating systematic burning did not occur. The Salish and Kootenais roamed a vast territory and there apparently was little need to plan or manage fires.

FIRE HISTORY INVESTIGATIONS

Methods

I used several methods to determine Indian fire influence on lower-elevation forests dominated by ponderosa pine, Douglas-fir, or western larch. The major approach was to compare fire history in 10 pairs of old-growth stands, one of each pair located in an area of past Salish and Kootenai habitation (hereafter, "heavy-use" stands), the other in an area remote from concentrated use ("remote" stands). Heavy-use stands were usually located in forests bordering large intermountain valleys and remote stands were usually in secondary canyons stemming from valley tributary canyons. Stand size ranged from about 200 to 600 acres (81 to 243 ha.) and stands were paired on the basis of similar vegetation potential (habitat types as per Pfister et al. 1977), elevation, and aspect. Figure 1 shows sample stand distribution.

In each stand, five to seven of the oldest trees with the most basal fire scars were sectioned with a chain saw (Arno and Sneck 1977). This sample number was usually sufficient to document most fires of appreciable size, provided sample trees were well distributed in the stand. I determined fire years from each cross-section in a laboratory and correlated fire years among the sample trees in order to develop a master fire chronology for each stand. A fire chronology was considered to begin when at least two sample trees started to record fires.

I calculated mean fire-free intervals (MFFI) for each stand as follows. Three identical periods for comparing fire frequencies were assigned each pair of stands. The beginning date of the first period was defined as the latest beginning date among the two stands' chronologies (for example, if stand A's chronology began in 1500 and stand B's began in 1600, then 1600 is the mutual beginning date). Two ending dates, 1860 and 1910, were assigned all stands in order to examine fire history for these important periods: 1) the pre-1860 (pre-settlement) era, 2) 1861-1910 (settlement period), and 3) 1911-1980 (fire suppression period).

A secondary study approach was to closely examine each fire scar with a microscope to see if the season of fire occurrence could be determined. Informants said Indians set most purposeful fires in spring and fall, whereas USDA Forest Service regional data show that nearly 80 percent of lightning fires occur in July and August (Barrows et al. 1977). It was hypothesized that the position of clearly-initiated scars relative to ring structure might show that fires occurred either during earlywood (approximately May 1 to July 1) or latewood (July 1 to September 15) formation, or during the dormant period (September 15 to May 1) in western Montana (E. Burke, Wood Technologist, University of Montana, Missoula, personal communication). This investigation in progress and results will be reported at a later date.

I used a third method to characterize the extent to which Indian fires augmented lightning fires. This approach involves uncontrollable variables and may be the least promising of the methods used. Two sites were intensively sampled in the Bitterroot Valley, the ancestral territory of the Salish as early as 6,000 years ago (Malouf 1974). The objective was to compare MFFI during two time periods in the same stand to see if the MFFI are similar. I assumed lightning fire frequency to be relatively similar during both periods. The periods considered were: 1) the pre-settlement (pre-1860) era--when lightning and Indians were the only ignition sources; and 2) 1931-1980--when lightning is the major causal factor and detailed records of all caused fires are available. The two sites, Goat Mountain and Onehorse Ridge, are especially suited to this approach because: 1) informants and journals indicate Indian fires often occurred in the Bitterroot Valley before 1860; 2) fire suppression records are complete back to 1931; this allows both estimation of mean lightning fire frequencies for 50 years and elimination of man-caused fires from the calculations; and 3) both sites are triangular faces of ridges that slope downward into the Bitterroot Valley and are topographically isolated by large, cliffy, glacial canyons; the possibility of lateral fire spread from other locations, which would tend to increase pre-1860 mean frequencies, is thus markedly reduced.

Twelve or more samples each were collected from Goat Mountain (about 300 acres [122 ha.]) and Onehorse Ridge (about 600 acres [243 ha.]). Pre-1860 MFFI were determined according to the methods described by Arno and Sneck (1977).[3] Modern mean lightning frequencies were estimated by first examining Bitterroot National Forest maps and documenting total ignitions per stand since 1931. Both sites are fully visible from the valley and Forest Service ranger stations, making records very accurate. It was then necessary to subjectively determine which fire-starts might logically have developed into spreading fires if there had been no suppression. I did this by examining Forest Service Individual Fire Reports (Form 5100 series), using date of ignition, fuel types, slope, aspect, position on slope, fire weather data, and nature and duration of each "fire" as decision criteria. I also examined National Weather Service daily temperature and precipitation data for one week before and two weeks after each ignition (weather stations are within ten miles of each sample site). After estimating the total number of potential fires I calculated expected MFFI by dividing the number of fire intervals into 50 years.

Results/Discussion

Nine hundred forty-six scars from 120 samples revealed 472 individual fires. Ponderosa pine was by far the superior species for high quality scar samples (95 of 120 cross-sections were from this species). I was often able to date unbroken fire sequences from about 1600--the earliest recorded fire was 1443. However, 1700 was the most common approximate beginning date for comparison of paired stand chronologies.

Paired Stand Comparisons

Pre-1860 Fire Frequencies.--Lightning or Indians were essentially the only ignition factors in western Montana before 1860. MFFI for the period were substantially shorter for nine of ten heavy use stands than their remote mates (table 1).[4] Six of the nine heavy-use stands had about twice the incidence of fire (fig. 2). Other studies (Buck 1973; Arno 1976; Dorey 1979; Gruell et al 1980)[5] document similarly short, usually single digit, MFFI for the same forest types in past Salish and Kootenai "heavy-use" areas. I have not found any studies that examine fire history in what can be considered "remote" areas.

I also calculated median fire-free intervals (not listed in table 1). In this case four of the nine heavy-use stands with higher frequencies had about twice as many fires.

In general, the maximum individual fire intervals for most stands did not exceed 35 years althoug three remote sites had intervals of 59, 62, and 64 years. I interpreted the shortest fire interval to be one year, but such short intervals are difficult to identify.

One possible reason heavy-use stands had shorter MFFI than remote sites is that stands in open valleys may have been prone to record both stand-specific fires and fires which spread in from other locations. Side canyon (remote) stands may have been more likely to only record fires ignited in the immediate vicinity because these sites are often bordered by fire barriers such as streams and inflammable vegetation. However, it seems doubtful that such large MFFI differences could be entirely attributable to this factor. The evidence suggests Indians were a major contributing factor in these differential frequencies. Later in the analysis, I will examine the feasibility of statistical testing to determine the probability

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[3] The Onehorse Ridge sample site and data for the pre-1860 period are from Arno (1976).

[4] The only remote stand with a higher incidence of fire than its heavy-use mate may be a function of poor site selection. Hot springs in the vicinity of the remote stand are known to have been attractive to the Salish (cf. Two Bear and McCartney Creeks).

[5] Gruell, G.E., W. Schmidt, and S. Arno. 1980. Seventy years of vegetation change in a ponderosa pine forest in western Montana. (Review Draft). USDA For. Service INT.

Table 1.--Mean fire-free intervals (MFFI) and fire interval ranges for 10 paired stands in western Montana, according to 3 time periods.

		(x)-1860[a]				1861-1910[b]				1911-1980			
		Heavy Use		Remote		Heavy Use		Remote		Heavy Use		Remote	
Paired Stands	Mutual Beginning Date	MFFI	Range	MFFI	Range	MFFI	Range	MFFI	Range	MFFI	Range[c]	MFFI	Range
FC/RAC	1776	8.4	2-13	42.0	5-59	8.3	3-15	10.0	4-11	35.0	7-35	17.5	9-33^{+}
MC/CG	1697	8.6	2-19	23.3	6-38	25.0	3-21	12.5	2-16	*(1889)	69^{+}	11.9	2-18^{+}
SC/ROC	1704	7.4	3-12	17.3	6-64	8.3	1-9	16.6	10-20	23.3	6-26^{+}	*(1890)	69^{+}
GM/SLC	1737	6.8	3-11	15.3	3-22	5.5	1-6	25.0	9-30	17.5	5-36^{+}	35.0	17^{+}-51
F/DC	1797	7.0	3-11	15.7	4-20	8.3	4-12	10.0	4-21	35.0	7-32^{+}	†(1939)	28-41^{+}
HAC/TC	1700	8.4	3-15	16.0	4-62	16.6	2-35	16.6	4-25	23.3	15-33^{+}	*(1901)	69^{+}
HC/HT	1722	10.6	5-19	19.7	5-43	10.0	4-19	16.6	5-31	23.3	4-26	35.0	4-31^{+}
HH/NB	1710	8.3	2-32	13.6	5-23	6.2	3-14	16.6	7-16	17.5	7-27^{+}	35.0	4-49^{+}
IT/RC	1695	12.7	3-35	16.5	6-36	12.5	6-16	16.6	6-30	35.0	8-36^{+}	†(1918)	7-62^{+}
McC/TB	1729	13.1	5-26	10.1	5-26	7.1	3-15	10.0	5-18	23.3	9-48^{+}	*(1896)	69^{+}
Mean (all stands)		9.1	±2	18.9	±9	10.8	±6	15.0	±5	25.9 (9 stands)	±7	26.9 (5 stands)	±11

[a] General date of beginning of white settlement in western Montana

[b] General date of beginning of modern fire suppression in western Montana

[c] "+" indicates interval length to 1980; number is either shortest or longest interval in period

*no fires occurred in the period; date in parentheses indicates last fire year

†only one fire occurred in the period; date in parentheses indicates fire year

Sample Stand Key:

FC - Fivemile Cr.	SC - Sixmile Cr.	F - Fairview	HC - Hughes Cr.	IT - Indian Trees
RAC - Rainy Cr.	ROC - Rock Cr.	DC - Doak Cr.	HT - Hog Trough Cr.	RC - Railroad Cr.
MC - McCalla Cr.	GM - Goat Mountain	HAC - Hay Cr.	HH - Hog Heaven	McC - McCartney Cr.
CG - Cutoff Gulch	SLC - Sleeping Child Cr.	TC - Thompson Cr.	NB - North Bassoo Cr.	TB - Two Bear Cr.

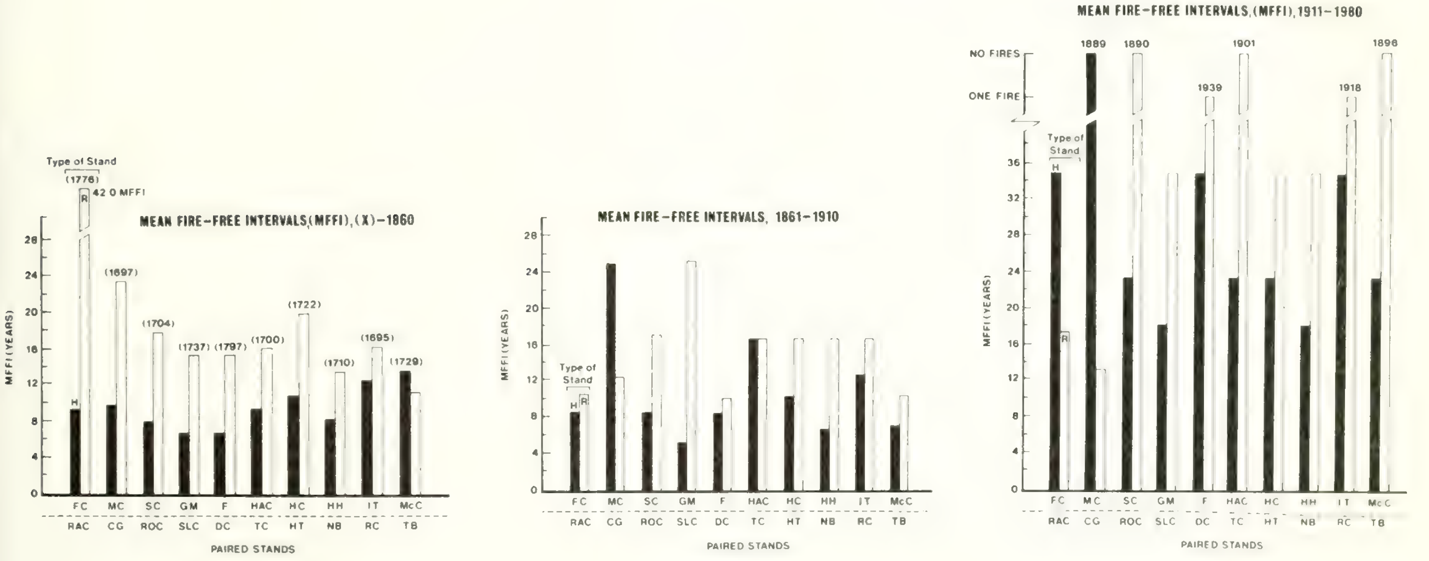

Figure 2.--Time period comparisons of Mean Fire-Free Intervals for 10 paired stands in western Montana (Heavy-use stands: ▮ Remote stands: ▯)

of any chance differences between heavy-use and remote stand MFFI.

The Period 1861-1910.--Informants and journals indicate Indian fires still occurred in western Montana until the beginning of the 20th Century but presumably to a much lesser degree. However, prospectors and others caused many fires in the region in the late 1800s (Ayers 1899; Lieberg 1899). This apparently occurred up until at least 1910, when organized fire suppression aimed at eliminating all fires in the region. MFFI were highly variable for this 50 year period (table 1). Fire occurrence decreased in 40 percent of the heavy-use stands and increased in 50 percent of the remote stands. Eight of ten heavy-use stands had shorter MFFI than remote sites, however, differences are smaller compared with pre-1860 figures. Three of the eight heavy-use stands with shorter MFFI burned more than twice as often as remote stands, one stand pair had equal amounts of fire, and one remote stand received twice as much fire as its heavy-use mate (fig. 2). Median intervals do not differ markedly from means for this period.

Several explanations are possible for such high variability. First, the shortness of the 50 year period may be conducive to variable means--longer time periods usually allow better characterization of fire history. Second, stands in open valleys probably were still subjected to more man-caused and unobstructed lightning fires. However, man-caused fires came into disfavor by settlers toward the end of the period, so some frequency reduction might be expected in heavy-use stands. Conversely, the increase in remote stand fires may have been due to prospectors frequenting back-country areas where these stands are located. Apparently prospectors set fires with the goal of destroying vegetation to expose mineral outcrops (Lieberg 1899).

Although the data indicate a shift in MFFI between heavy-use stands and remote stands compared with the previous period, there was little change in overall fire occurrence in the region. These data do not support Wellner's (1970) hypothesis that high man-caused and lightning fire frequencies from 1860 to 1935 were unprecedented in Northern Rocky Mountain forests.

The Period 1911-1980.--The data show a substantial increase in MFFI for most stands following the advent of modern fire suppression (fig. 2). Suppression practices became well organized and quite effective throughout the region in the 1930s. Twelve of the 20 stands had MFFI of 35 years or more (table 1). Median calculations are not meaningful for this period due to infrequent fires. In general, heavy-use stands still received slightly more fire than remote sites, perhaps reflecting modern man-caused fires (shorter MFFI from unobstructed lightning fires is no longer a plausible explanation due to efficient suppression). Mean intervals in the 12 stands now equal or exceed the longest individual fire intervals before 1910 for most stands. These results are similar to those of other fire history analyses done in the region (Wellner 1970; Buck 1973; Habeck and Mutch 1973; Loope and Gruell 1973; Arno 1976; Gabriel 1976; Dorey 1979; Tande 1979; Arno 1980; Gruell et al. 1980[5]), however, several of my stands still show relatively short MFFI since 1911. The general reduction in fire frequency is illustrated most dramatically by the McCalla Creek heavy-use stand. Before 1860, fires occurred on an average of every 8.6 years but sample trees have not recorded a fire for the last 91 years.

Goat Mountain/Onehorse Ridge Period Comparisons

Six lightning ignitions occurred on Goat Mountain from 1931 to 1980. After examining fire reports and weather data, I concluded that three or four fire-starts had the potential to spread. This would result in an expected MFFI of 16.6 to 12.5 years. The MFFI from 1700 to 1860 for the same stand was 6.7 years.

Seven lightning ignitions occurred on the Onehorse Ridge site during the modern period. The data suggest that as many as five of these might have become spreading fires, for an expected MFFI of 10.0 years. Arno's (1976) data show a MFFI of 5.1 years from 1700 to 1860.

One inherent weakness of this approach is that an "error" in judgement of just one or two potential fires can result in large discrepancies in expected MFFI because the 50-year period is relatively short. However, my estimates of potential fires are conservative, and, if anything, represent an over-estimation of the number of expected fires for both sites. Data from wilderness fire management areas in USDA Forest Service Region One indicate that fewer than 50 percent of lightning ignitions have potential to develop into spreading fires (Division of Aviation and Fire Management, Missoula). Thus, the differentials between pre-1860 MFFI and modern possible MFFI for the two sites may actually be larger than indicated.

CONCLUSION

The paired stand method appears to have the most potential for characterizing the Indian role in an area's fire history. Each approach has limitations. Nevertheless, the combination of informant, historical, and biological data may present the best current means of research into this difficult problem.

This study revealed substantial fire frequency differences in pre-settlement ponderosa pine/Douglas-fir forests in western Montana. The data suggest that the Salish and Kootenai Indians were largely responsible for causing the high frequencies characteristic of stands in habitation zones. After further analysis, I will report on the ecological effects and possible management implications of such frequent fires in this forest type. Perhaps future studies will examine, in detail, what these different frequencies can mean in terms of such management concerns as forest productivity, composition, and protection.

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Fire History of Kananaskis Provincial Park — Mean Fire Return Intervals[1]

Brad C. Hawkes[2]

Abstract.--Mean fire return intervals for different ecological subzones, aspects and elevations in Kananaskis Provincial Park were described. Comparison of the results from this study with others was not practical because of a number of constraints. A discussion of the mean fire return interval results and park resource management was presented.

INTRODUCTION

Fire has played an important role in the ecology of northern Rocky Mountain forests (Habeck and Mutch 1973). Fire history studies in Alberta have indicated that fire return intervals, sizes and intensities have varied in different forest ecosystems (Byrne 1968; MacKenzie 1973; Tande 1979). Fire history information is an essential element in describing forest ecosystems, development of resource management alternatives, and implementation of programs in fire management planning and operations (Arno 1976).

Kananaskis Provincial Park (KPP) was selected for this study because intervals, sizes and intensities of fires in high elevation (>1500 metres) forests of the Canadian Rocky Mountains have not been investigated in detail. In addition, the recent creation of KPP provided an opportunity to include the collection of fire history information as part of the overall resource inventory of the Park.

In this paper, I will present only part of the results of this study. The paper will focus on the mean fire return intervals (MFRI) of high elevation forests in KPP. A fire chronology, fire-year maps and a stand origin map are presented in an earlier paper (Hawkes 1979).

The purpose of this paper is to describe the MFRI for different ecological subzones, aspects and elevations in KPP. A discussion will also be included on how this information on MFRI might be utilized by park resource planners in KPP.

THE RESEARCH AREA

The research area is located approximately 120 kilometres southwest of Calgary, Alberta at the head of the Kananaskis Valley (Figure 1). KPP, in which this study was conducted, encompasses 508 square kilometres, of which 236 sq km is forested. Elevation of the forested land ranges from 1525 metres at the valley bottom to 2300 metres, the approximate treeline.

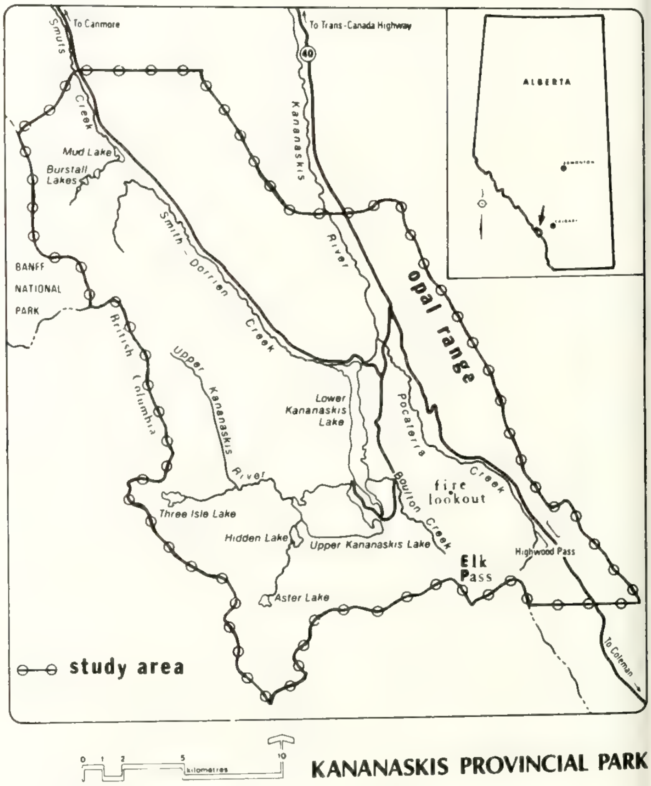

Figure 1.--Location of study area.

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[1] Paper presented at the Fire History Workshop, Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz., October 20-24, 1980.

[2] Brad C. Hawkes, Fire Research Officer, Pacific Forest Research Centre, Victoria, B.C.

Summer (June to September) temperature and precipitation records are available for Kananaskis Fire Lookout (elev 2072 m), operated by the Alberta Forest Service for the period 1966 to 1975. Figure 2 illustrates the monthly mean temperature and precipitation for the summer at Kananaskis Fire Lookout. Jaques (1977) indicated that the climate within the Park represents a fairly narrow range of the total Rocky Mountain east slopes climatic regime, being skewed toward the moist-cool end of the gradient.

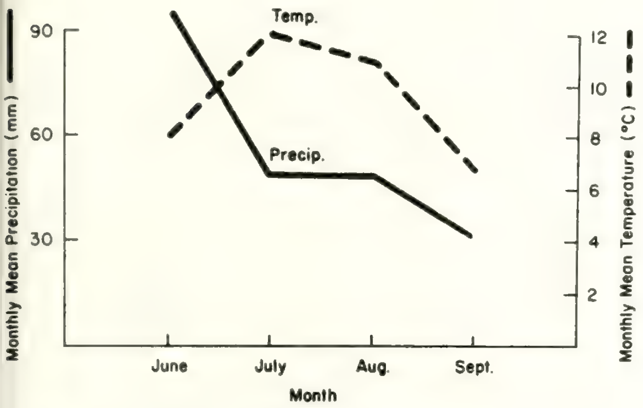

Figure 2.--Monthly mean temperature and precipitation for the summer at Kananaskis Fire Lookout (based on data for the period 1966-1975).

The vegetation of KPP is classified in the subalpine ecological zone according to the ecosystem classification described in Walker *et al.* (1978). This zone is divided into upper and lower subalpine subzones based on the occurrence of certain vegetation types and differences in vegetation physiognomy which reflect macroclimate. The lower subalpine subzone occurs generally below 2000 metres' elevation. The upper subalpine subzone ranges from 2000 to 3000 metres.

Mature Engelmann-white spruce hybrid[3] (*Picea engelmannii* Parry x *P. glauca* (Moench) Voss.) - subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests occur in the higher elevational areas of the lower subalpine subzone. Successional lodgepole pine (*Pinus contorta* Loudon var. *latifolia* Engelm.) forests dominate the rest of the lower subalpine subzone.

The upper subzone is transitional between the lower subalpine subzone and the treeless alpine zone. Engelmann spruce, subalpine fir and alpine larch (*Larix lyallii* Parl.) are common in this subzone. Closed forests are common at the lower elevational areas of the subzone. Tree islands are common, with heather (*Phyllodoce* sp.) meadows occurring between them at the higher elevational areas of the subzone.

For at least 8,000 years man has occupied the Kananaskis Lakes area, with most early use concentrated between 5,000 B.C. and 200 A.D. (Aresco Ltd. 1977). The Stoney Indians moved to the Kootenay Plains and Morley area in the early 1800s. They travelled through the Kananaskis Valley on hunting trips to British Columbia.

The Kananaskis Lakes area had seen relatively light use by man and had escaped extensive development until the recent construction of the facilities for KPP. Recreation use was limited until the improvement of the Kananaskis trail to facilitate the construction of dams in the 1940s at the lakes. Paved access to the Park (completed in 1978) resulted in a marked increase in the number of visitors to the lakes area.

METHODS

The fire history of KPP was documented, using a fire-scar analysis, a stand age-class inventory, examination of historical and Alberta Forest Service fire records, and interpretation of aerial photographs.

The approach used in the field to document the fire history of KPP varied from that suggested by Arno and Sneck (1977). A network of reconnaissance transects were not used. Sample points for the fire history study were established along the stand edge and within remnant stands which provided the best source of fire history information. Many stands which contained fire history information were a hectare or less in size, perhaps because of the high intensity of past fires.

Snags provided a secondary source of information which extended the fire chronology to earlier fires than could be dated from fire scars on living trees. Data were collected from standing snags and dead down logs on the forest floor. Four problems were encountered when snags were used to obtain fire history data.

These were:

1. Weathering of the tree's exterior caused fire dates to be incorrect up to 10 years.
2. Determining which fire killed the snag was sometimes difficult; cross-dating to other living and dead fire scar information was necessary.
3. Sometimes the snag died a number of years after a fire scorched its crown.
4. Trunk rot added to aging problems.

The large expanse of young, even-aged stands in KPP made it necessary to use snags if historic fire years were to be determined.

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[3] Called Engelmann spruce in this paper.

A "master fire chronology" of KPP was developed from fire-scarred tree wedges, age-class data and Alberta Forest Service records according to the procedure in Arno and Sneck (1977). A total of 142 fire scars and 705 increment cores were taken on 117 fire history plots to establish the fire chronology. This information was used to estimate the MFRI for each fire history sample site in KPP.

RESULTS AND DISCUSSION

Mean fire return interval (the average number of years between fires) has been expressed in the literature in two different ways. The first is based on the average number of years between fires for a given study area (e.g. KPP, Jasper National Park or a particular watershed). The second is based on the average number of years between fires for a given point or stand (usually less than 100 ha) within a study area. The first expression of MFRI is area-dependent, because it will shorten if the size of the study area is increased. The point expression of MFRI is more useful for comparing results from one study area to another.

MFRI was calculated on a point basis to determine the effect of elevation, aspect and ecological subzone on MFRI. A two-way analysis of variance was done for elevation and aspect (Table 1). Twelve plots were randomly picked for each cell for the analysis of variance. The elevational differences were significant at the 95% probability level. The MFRI for the north aspect was significantly different at the 95% probability level from the south, west and east aspect (Table 1). Fire history plots were stratified according to their location (lower (n=88) or upper subalpine (n=13) subzones). A "t" test of the means indicated that the two ecological subzones had significantly different MFRI at the 95% probability level (Table 1). The results for elevation, aspect and ecological subzone were:

Elevation	MFRI (years)
1525-1830 m	90
1830-treeline (Approx. 2300 m)	153

Aspect	MFRI (years)
North	187
South	104
West	101
East	93

Ecological Subzone	MFRI (years)
Lower Subalpine	101
Upper Subalpine	304

Comparison of MFRI results from different studies is possible if the following conditions are met:

1. MFRI is calculated on a point or stand basis (usually 41-81 ha (100-200 ac) in size).

2. The study areas have the same vegetation communities (e.g. habitat types as described by Pfister et al. (1977) for Montana) not just the same vegetation zone or subzone (e.g. forest series as described by Pfister et al. (1977)).

3. Arno (1980) mentions the importance of the distribution of forest series on the landscape. Small isolated forest series which are surrounded by a major forest series may have a MFRI similar to the major forest series.

4. The length of record of fires and the study approach are similar for the different studies (Arno 1980).

5. Each area had a similar man-caused fire history (e.g. Indian fires).

Table 1.--ANOVA table for two-way analysis of variance (elevation and aspect vs MFRI), Scheffe multiple comparison results for aspect means and "t" test results (ecological subzone vs MFRI).

Source	Sum of Squares	Degrees of Freedom	Mean Square	Computed F	Probability
Elevation	96610.50	1	96610.50	6.38	.025*
Aspect	140989.30	3	46996.43	3.10	.050*
Interaction	94147.00	3	31382.33	2.07	>.100
Error	1332866.75	88	15147.35		

* significant according to the confidence level set in this study (95%)

Scheffe multiple comparison (95% confidence level) indicated that the difference between aspect means had to be >83.9 to be significant.

"t" Test Results

	Mean	Variance (S^2)	No. of Observations
Upper Subalpine Subzone	304	5768.8	13
Lower Subalpine Subzone	101	13329.6	88

Common Variance (S^2p) = 12539.52

Value of t = 6.101

Critical T is >1.645 at 95% confidence level, therefore t is significant.

Comparison of my MFRI results with other study areas will not be made because of these constraints.

Most fires in the lower elevation sections of KPP (<2000 m) seemed to have been large (>1000 ha), stand-destroying fires of medium to high fire intensities, with low to moderate fire intensities on the edge and backing sections. Development of recreation facilities in the Lower Kananaskis Valley of KPP has led to a policy of total suppression on all fires. To re-introduce the same type of fire to KPP would not be possible now. Prescribed burning on a small scale might be a possible alternative. If so, how large an area of forest and which areas should be burned each year? The reciprocal of the point estimate of MFRI will give the average proportion of the whole area burned annually (Van Wagner 1978). This proportion would give a long-range average to work toward if the MFRI is accepted as the optimum fire cycle. Van Wagner (1978) describes the optimum fire cycle as that which "maintains the forest in question in the best possible ecological state, from the various viewpoints of production, health, and competition with other vegetation types that would tend to supplant it in the absence of fire."

To answer the question of where to burn is also difficult. The historic age-class mosaic would be difficult to maintain because of the constraint on large fires. From the theoretical viewpoint of the fire return interval, the actual number of fires and their individual sizes are unimportant; only the total burned area per year counts (Van Wagner 1978). Many small sized fires will still maintain the age-class distribution. Only after a detailed study of the ecosystems in question throughout their entire age range can we start to answer the question of where to burn and how much (Van Wagner 1978).

These questions on when, where and how much fire will be allowed or can be logistically handled by the resource staff will have to be answered. Only 20 lightning fires out of 126 were allowed to burn in the Selway Bitterroot Wilderness in 1979[4] because of the commitment of fire suppression forces and the prescription limits of fire weather outlined in the fire management plan. This does not allow for the natural fire regime to be totally re-introduced because the fire agency cannot handle the fire load. Perhaps the historic average burned area per year might be set as a long-range goal.

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Interpretation of Fire Scar Data from a Ponderosa Pine Ecosystem in the Central Rocky Mountains, Colorado[1]

R. D. Laven, P. N. Omi, J. G. Wyant and A. S. Pinkerton[2]

Abstract.--Fire scar data from twenty ponderosa pine trees located in the Central Rocky Mountains, Colorado, were used to determine fire frequencies by historical era, fire size, topographic position and slope aspect. The average mean interval between fires is somewhat larger than in other parts of ponderosa pine's range.

INTRODUCTION

Prior to the arrival of European man to North America, creeping surface fires were a common occurrence in ponderosa pine (Pinus ponderosa Laws.) forests (Kotok 1934, Wagener 1961, Biswell 1972). These fires had a significant effect on stand structure and composition by eliminating understory reproduction and enhancing regenertion within forest openings. The result was an uneven-aged forest with trees growing in even-aged groups (Biswell 1972, Gartner and Thompson 1972, Wright 1978). Previous studies indicate that fire frequency varies in these forests depending on study area location. Weaver (1951) found the frequency in Arizona and New Mexico to be between 5 and 12 years. Show and Kotok (1924) and Wagener (1961) determined an average frequency of 8 to 10 years in California. Arno (1976) reported an average frequency of 6 to 11 years for mature ponderosa pine in western Montana and eastern Idaho.

Little is known, however, about natural fire frequencies in the ponderosa pine forests of the central Rocky Mountains. Daubenmire (1943) indicates that slow spreading surface fires were quite common but does not attempt to quantify their frequency. Wright (1978) speculates that fire may be less frequent in this region since litter is usually meager, canopy coverage is generally no more than 25% (Daubenmire 1943), and fine fuels appear to be less than in other parts of its range. In the only quantitative study to date, Rowdabaugh (1978) indicates an average fire frequency of 84 years prior to the initiation of fire suppression, and 110 years for the entire fire chronology.

In this study we have determined the mean time interval between fires in several ways as our data tend to support Kilgore and Taylor's (1979) viewpoint that a single mean time interval is misleading. We calculated fire frequencies based on the historical time period, the size of the fire, the topographic position, and the slope aspect.

Study Area

The study area is a 50 ha ponderosa pine forest located in Wintersteen Park in the Front Range of the Colorado Rocky Mountains, approximately 2 km northeast of Rustic, Colorado in the Roosevelt National Forest. Lying in a level to steeply sloping tertiary drainage of the Cache la Poudre River, the study area ranges from 2500 m to 2800 m in elevation. Numerous outcroppings of Precambrian granite occur throughout the area. The soils are rocky loams of the Wetman-Boyle-Moen complex. These are shallow, well-drained soils of steep to gentle mountain slopes (USDA Soil Conservation Service, unpublished).

METHODS

The primary objective was to determine site-specific fire history for the study area. For this reason, all intact fire-scarred trees in the location were sampled. Lightning-scarred trees, and trees that showed evidence of previous scarring but were healed over, were not included in the sample. As a result, we examined 20 trees that encircled the study area.

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[1] Paper presented at the Fire History Workshop, University of Arizona, Tucson, October 20-24, 1980. The research reported here was approved and financially supported by the Eisenhower Consortium for Western Environmental Forestry Research.

[2] Assistant Professor, Associate Professor, Graduate Research Assistant and Forestry Technician, respectively, Dept. of Forest & Wood Sciences, Colorado State University, Fort Collins ,CO.

Wood sections were removed from the base of each scarred tree using the method described by McBride and Laven (1976). Each tree was aged and its location was recorded on a topographic map. Fire dates were determined for each tree by counting the number of annual growth rings from the sampling year (1980) to the last (most recent) scar, and between previous scars on each wood section.

Cross-dating techniques were used to reduce the possibility of dating errors and to account for potential complications such as missing rings, double or false rings or anomalous rings associated with fire scarring. Skeleton plots (Stokes and Smiley 1968) were constructed for each specimen and used to develop the master fire chronology. Since scars, however, are not caused by every fire and more recent fires can consume the evidence of earlier fires, the recorded scars represent a conservative estimate of the number of previous fires.

For each individual tree the mean interval between scars was determined. These values were used to calculate the average mean interval for all of the trees as a function of aspect, topographic position, historical era and fire size. Additionally, we compared the average mean intervals using our formulation with the results generated using Houston's (1973) formulation.

Ring widths for each individual for three years prior to each scar were compared to the mean ring width of the previous ten years to investigate the supposition that fires in this region are preceded by several years of drought. An optical micrometer mounted to the eyepiece of a dissecting microscope was used to measure the ring widths to .0005 mm.

Finally, a stand-age analysis was performed to determine if the age-class destribution found on our study site was a typical ponderosa pine mosaic of even-aged groups. Two increment cores taken at ground level were prepared in the lab and examined under a dissecting microscope to determine tree age; tree ages were compared to fire scar dates to assess the degree of correspondence.

RESULTS AND DISCUSSION

Fire Chronology

The range in fire scar dates covered a period from 1708 to 1973. Because the mean age of the sampled trees was 248 years and the mean age of the trees when initial scarring occurred was 81 years, relatively few scars (21.1%) occurred prior to the mid-1800's. Mortality, and consumption of scars by subsequent fires would also contribute to this low percentage. Between the beginning of the settlement in the mid-1800's until the inception of fire suppression at the turn of the century, 65.4% of the scarring occurred. The remaining 13.5% of the scars were recorded during the suppression era.

Fire Frequencies

Table 1 presents a summary of our determinations of fire frequency. The average mean interval between fire scars for all sampled trees throughout the entire chronology is 45.8 years. This frequency compares to Rowdabaugh's (1978) figure of 110 years. The apparent disparity in results is considerably lessened if the data are uniformly analyzed. For example, if we use Houston's (1973) formula for fire frequency (used by Rowdabaugh) our frequency becomes 129.9 years. On the other hand, if we use Rowdabaugh's data and calculate the frequency as the mean interval between fire scars (our method), his frequency becomes 37.9 years. Rowdabaugh's pre-suppression figure of 84.0 years likewise becomes 38.9 years. Either way, the results are much closer. Houston (1973) incorporates the entire age of the tree in determining the frequency, whereas we consider only the intervals between fire scars. The difference, then, is that Houston's (1973) formula includes the time it takes for initial scarring and the time

Table 1. Average Interval Between Fire Scars in Years (Wintersteen Park, Colorado)

	$\bar{x}$ (min-max)
Entire Chronology (n = 20)	45.8 (3-161)
Slope Aspect	
South (n = 18)	34.9 (3-161)
North (n = 2)	64.3 (5-157)
Topographic Position	
Lower Third (n = 5)	37.5 (5-157)
Middle Third (n = 5)	35.7 (3-105)
Upper Third (n = 5)	37.9 (5-114)
Historical Era	
Pre-1840 (n = 6)	66.0 (5-157)
1840-1905 (n = 12)	17.8 (3-161)
Post-1905 (n = 3)	27.3 (8-46)
Fire Size	
Small (n = 9)	20.9 (11-145)
Large (n = 12)	41.7 (5-63)

since last scarring (in our case an average of 81.3 and 91.6 years, respectively). Since unscarred trees are not as sensitive to scarring by low intensity fires as previously scarred trees (Kilgore and Taylor 1979, Gill 1974, Lachmund 1921), including this relatively insensitive period when calculating fire frequency may be misleading.

As previously suggested, we feel that a single mean interval is not an appropriate representation of fire frequency. We therefore calculated the mean interval for a variety of circumstances. We emphasize, however, that by so doing we reduce an already small sample size with considerable inherent variability. Consequently the results should be viewed as only indications of trends.

The mean fire frequency for trees occurring on south-facing slopes is 34.9 years which compares to 64.3 years for north-facing slopes. The north-facing interval is based on a sample of only two trees; the dearth of sample trees in itself is indicative of the variation in frequency associated with slope orientation.

In spite of a 300 m elevational change, fire frequencies are essentially the same (less than 2 years difference) for the lower third, middle third, and upper third of the slope. Analysis of fire sizes (discussed subsequently) indicates that these similarities are not due to individual fires burning entire slopes.

Based on the history of land use in the general area (Swanson 1975), three eras were distinguished which provide a more realistic indication of past fire frequency. The pre-settlement era (pre-1840) revealed a mean interval of 66.0 years; the settlement era (1840-1905) had a mean interval of 17.8 years; and the suppression era (post-1905) has a mean interval of 27.3 years. Since these eras encompass different spans of time, another approach is to compare the number of fire scars per 100 annual rings of growth (Kilgore and Taylor 1979). For these three historical eras, the respective figures are 8.3, 52.3, and 9.3. The large differences in frequencies associated with these historical eras only serve to underscore the need to interpret average fire frequencies with caution.

In order to compare frequencies by fire size, two general size categories were distinguished. The "small" fire size category represented fires that scarred single or small groups of trees in close proximity. Such fires were on the order of 1 ha in size. The "large" fire size category represented fires that scarred trees on at least two opposing slopes, and were approximately 25 ha in size. Approximately half of the fires fell into each category. There is no evidence to suggest that a single fire burned the entire study area. Using fire incidence as our measure of frequency in this case, the small fires occurred on the average of every 20.9 years and the large fires every 41.7 years. It is noteworthy that during the settlement era, the mean incidence of large fire occurrence was 16.3 years.

Tree Ring Widths

Analysis of average tree ring widths three years prior to a fire scar did not reveal any significant narrowing. If a prolonged drought period is a precursor to fire occurrence in this region, the narrower ring widths would most likely precede large fires prior to the influence of settlement. However, regardless of historical era or fire size, ring width narrowing was not exhibited.

Stand-Age Analysis

Analysis of age-class distribution does not support the classic concept that ponderosa pine is found in small even-aged groups that are part of a larger uneven-aged forest. Our study area is indeed uneven-aged, but the suspected correspondence of stand age with time elapsed since fire is not found. Because of the open nature of this forest, successful seedling establishment may not be as strongly tied to the exposure of mineral soil (as a result of fire) as ponderosa pine forests with heavy litter loadings.

CONCLUSIONS

Fire history studies are often conducted to provide guidelines for fire management planning. We assume that the resultant fire frequencies reflect the 'natural role of fire' that helped shape the structure and composition of the area being studied. This assumption may not be valid and we are therefore compelled to interpret our results with caution.

Each historical era of our fire chronology is confounded to such an extent that interpretation is difficult. The pre-1840 portion of the chronology is not complete; the data become less reliable as you move back in time, and the role that Indians played cannot be adequately quantified. The settlement era is confounded by the impact of settlers, lumbermen, cattlemen, and others, and obviously the fire suppression era is impacted by our control technologies. Averaging over these time periods is not the solution; in fact averaging tends to further obscure the results.

Since most studies of this kind are fraught with similar difficulties, inter-study comparisons of results may be the most valuable aspect of this work. Our results indicate that the average mean interval between fires is somewhat longer in ponderosa pine forests of the central Rockies than in other geographical regions. Additionally, the fire regime is variable: longer interval "large" fires are superimposed on more frequent "small" fires. Finally, successful regeneration of ponderosa pine does not appear to be correlated with past fire occurrence.

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Fire History of Two Montane Forest Areas of Zion National Park[1]

Michael H. Madany and Neil E. West[2]

Abstract. A fire chronology for the last 480 years was developed from 119 partial cross sections of fire scarred ponderosa pine on a large plateau and a small, isolated mesa. Large fires (burning more than 400 ha) occurred nearly every three years prior to 1881 on the plateau. A sharp decline in fire frequency began thereafter, some forty years before the area was obtained by the National Park Service. The fire frequency of the relict mesa near the plateau featured an interval of 69 years. Changes in land use triggered the decline in fires on the plateau.

INTRODUCTION

Many researchers have documented a drastic decline in fire frequency in western coniferous forests in the last century. Ponderosa pine and mixed conifer forests have received considerable attention (Wright 1978). Reports of presettlement fire intervals range from almost yearly in northern Arizona (Dieterich 1980) to 17.8 years in certain situations in the Sierra Nevada (Kilgore and Taylor 1979).

Prior to this study, no detailed research had been conducted regarding the fire history of montane ecosystems in either Utah or the northern half of the Colorado Plateau. A survey by West and Loope (1979) found that fire was significant only at upper elevations within Zion National Park. Our project was funded by the National Park Service (NPS) as an extension of that prior work. The specific aim was to investigate historical changes in the fire regime of the upper elevation ecosystems in the park, and provide data to aid in the development of a fire management plan.

STUDY AREA

Research was focused on the 3640 ha (9000 ac) Horse Pasture Plateau (HPP). This rectangular 3 km (2 miles) by 13 km (8 miles) land mass is sharply demarcated on nearly all sides by sheer 150-300 m (500-1000') cliffs. The undulating surface of the plateau is dissected by 15 intermittent streams. Elevation ranges from 1980 m (6500') to 2380 m (7800'). A pristine, isolated mesa (Church Mesa) near the plateau was included in the study area to provide an analog that had no been logged or grazed by livestock. Church Mesa has soil , elevation, and topographical characteristics that are identical to the HPP which lies 2 km (1.5 miles) to the north. The intervening land is a barren expanse of sandstone cliffs and slickrock.

Most of the landscape of the two study areas is covered by either ponderosa pine forest or Gamb oak woodland. Mesic locales are occasionally dominated by mixed conifer forests or aspen grove Dry ridge crests and south-facing slopes are covered by pinyon-oak-juniper woodlands or servic berry-manzanita shrublands. Meadows are found in some of the major valley bottoms.

A range of past land use intensities was found on the HPP. The northernmost section was moderately logged in the 1950's. The northern half of the plateau was lightly logged from 1905 until 1922 in the vicinity of a road along the central ridge. The entire plateau was grazed by horses and cattle from 1863 until the 1920's. In the 1930's, the southern third of the plateau was fenced[3] and escaped much of the heavy sheep grazi that occurred throughout the rest of the region (Hinton 1961). It is unlikely that Church Mesa was scaled by humans before the last decade. However, this mesa does support populations of mule deer and cougar, thus providing the same ungulate-predator dynamics as the "mainland" plateau.

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[1] Paper presented at the Fire History Workshop (Laboratory of Tree Ring Research, University of Arizona, Tucson, October 20-24, 1980).

[2] Authors are, respectively, Graduate Research Assistant and Professor, Department of Range Science, Utah State University, Logan.

[3] Beatty, Reid. 1979. Interview. Toquerville, Utah.

METHODS

Data Collection

Catfaces were chosen for sampling on the basis of information value (number of scars) and wood quality (absence of ant infestations or visible rot). Since research was carried out in a de facto wilderness area within a national park, cutting was kept at a minimum. Therefore, when presented by a grove of pine, the tree with the most scars was chosen. Usually, the majority of trees were unscarred and only a few were multi-scarred, indicating the insensitivity of most ponderosa pine to fire. Even though scarred trees are more prone to subsequent scarring, only a minority of catfaces had more than a couple scars. Thus, less than 35% of all catfaces observed were cut.

Usable partial cross sections were taken from 119 fire-scared ponderosa pine, two white firs, one Douglas-fir and one Rocky Mountain juniper. Several cross sections were cut from Gambel oak, but were not datable due to heart rot. Cross sections were cut using the methods described by Arno and Sneck (1977). Physical site factors and plant community type were recorded for each sample tree and their location plotted on an aerial photograph. Permanent vegetation sampling plots with 15 x 20 m dimensions were established at 95 locations in a regular .4 km (.25 mile) grid pattern. Vegetation cover, tree density, and fuel load were measured in addition to physical site factors. Increment cores were taken from representative trees in various size classes within the plot (Madany 1981). Access to Church Mesa was gained by helicopter. Partial cross sections were cut and vegetation sampling plots were located in sites analogous to those in the main study area.

Data Analysis

Each section was planed and carefully counted with the aid of a dissecting microscope on two separate occasions. The date of each fire and the pith (or oldest ring in cases where pith was not reached) were recorded, and then organized into a master chronology. Raw dates were not assumed to be immediately accurate due to the problem of missing rings. Sooeriaatmadja (1966) reported that in an area of ponderosa pine in Oregon known to be burned in 1938, 10 stumps showed a 1938 date, while 17 indicated 1939, and 8 indicated 1940. Sections from Church Mesa showed a similar pattern of clusters of two to four "fire years" separated by wide intervals of fifty to seventy years with no scar dates. Therefore, cross dating had to be employed to minimize this inherent source of error. Cross-dating and subsequent adjustment of dates were done as conservatively as possible with an emphasis on back-dating isolated fire years to be in accordance with neighboring trees.

The terminology of Kilgore and Taylor (1979) was used to express the occurrence of fire. "Frequency" refers to the interval between fires for small areas of land, while "incidence" denotes the interval between fires over larger geographic units. Frequency was determined from both individual trees and clusters of trees that were assumed to have had identical fire histories because they were adjacent to each other. Each of the 26 clusters covered an area of .5-2.0 ha (1-5 ac) and was homogeneous with respect to physical site factors. Two larger clusters, termed groves, were also used to compute composite frequencies. They were 12 ha (30 ac) and 40 ha (100 ac), respectively, and provide the most accurate of all frequency values. The rationale behind the use of clusters is that a single tree rarely, if ever, records all the fires that burn around it. Thus, a composite frequency gives a more accurate and useful expression of frequency than values from lone trees (Kilgore and Taylor 1979).

Incidence was tabulated for 12 "watersheds" of 240 to 400 ha (600 to 1000 ac) in size, and four "plateau subdivisions" of 810 to 1220 ha (2000 to 3000 ac). The latter were comprised of two to four watersheds (fig. 1). Thus, the occurrence of fires through time was assessed at each of the six levels in this areal hierarchy (table 1). Sixty fires were extensive enough to scar at least five trees. The probable area of each of these burns was mapped using natural fire breaks (cliffs, sparsely vegetated ridgetops) as boundaries around each constellation of scarred trees.

Table 1.--Geographic units used to compute fire incidence and frequency on the HPP.

	Unit	N
Incidence	Plateau (or mesa)	2
	Plateau subdivision	4
	Watershed	12
Frequency	Grove	2
	Cluster	26
	Individual tree	123

RESULTS AND DISCUSSION

A precipitous decline in fires occurred on the HPP after 1881 (fig. 2). Records from the 16th and early 17th centuries are scanty due to a scarcity of trees that were alive then. By the end of the 18th century, virtually all sample

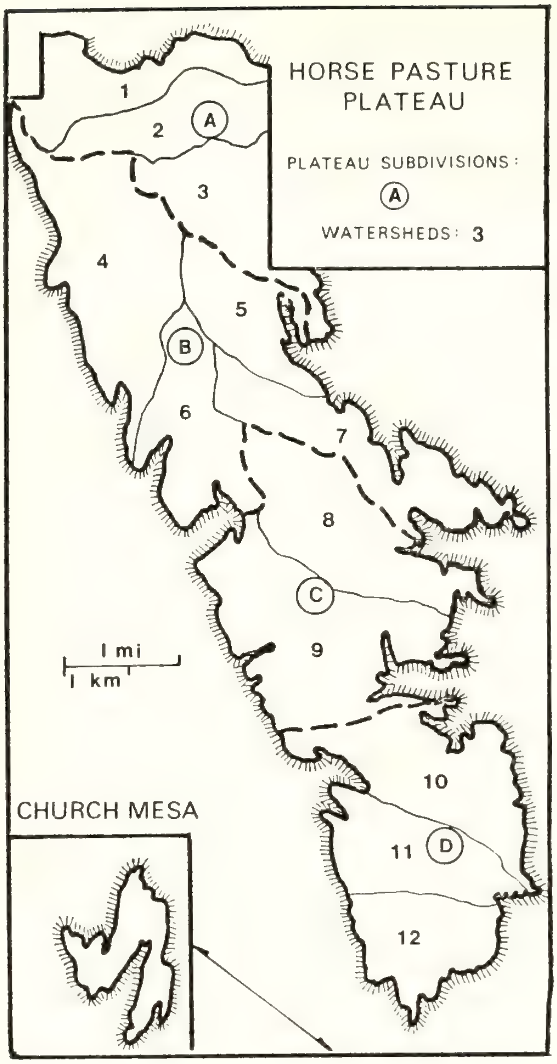

Figure 1. Map of the Horse Pasture Plateau and Church Mesa showing plateau subdivisions and watersheds.

trees had been established. The graph of "fire susceptible" trees in figure 2 is the cumulative representation of the initial scar dates of the sample population (sensu Arno 1976).

The following time periods will be used to organize the results. The Pre-European Period began in 1751 and ends in 1863 with subunits of 50 and 63 years. The time between 1864 and 1882 was deemed the Transition Period, when settlers began to graze livestock on the plateau, and the Paiute Indians were forced onto their reservation. The Grazing Period lasted from 1883 until 1925 and was the time when horse, cattle, and sheep numbers were at their highest. The National Park Service Period extended from 1926 until the present, and featured a phasing out of livestock grazing and the implementation of a total fire suppression policy (Madany 1981).

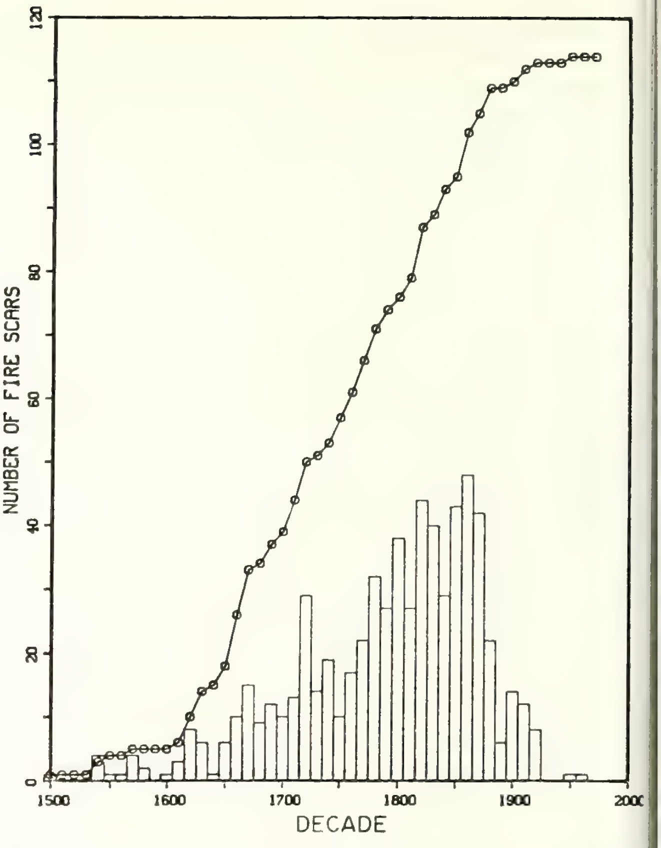

Figure 2. Histogram of fire scars per decade on the HPP. The curve records the recruitment of susceptible trees (a tree is considered susceptible after its first scar) to the sample population.

Fire Incidence

Plateau incidence

Starting with the most general situation of the total plateau, the fire scar record reveals a steadily increasing incidence of fire until the beginning of the Grazing Period (table 2). The last unit of the Pre-European Period is most representative and shows that in nearly every year, large enough fire occurred to have scarred one of the 123 sample trees. There was no essential change during the Transition Period. The seemingly high incidence of fire in the NPS Period is misleading. This figure incorporates

Table 2.--Fire incidence of the HPP.

	Time Periods				
	1751- 1800	1801- 1863	1864- 1882	1883- 1925	1926- 1980
Number of Fires	29	48	14	16	32
Incidence	1.7	1.3	1.4	2.7	1.7

Table 3.--Incidence of fires larger than 400 ha (1000 ac) on the HPP.

	Time Periods						
	1651-1700	1701-1750	1751-1800	1801-1863	1864-1882	1883-1925	1926-1980
Number of Fires	4	6	10	18	6	0	0
Incidence	12.0	8.3	5.0	3.4	3.0	-	-

28 recorded fires from the last 30 years, in addition to three fires that caused scarring on trees.[4] Only one of these 31 fires burned more than 4 hectares (10 ac).
in amount of area burned. The area of each of the 60 major fires was estimated and tabulated by year and historical period. Table 3 displays incidence of large (greater than 400 ha [1000 ac]) fires in the various periods. Overall, 26% of scar dates were from moderate to large sized burns. This estimate is quite conservative since many older dates from the 16th and 17th centuries probably represent larger conflagrations but natural mortality, and removal by logging, have reduced the data available. Table 4 presents the acreage of each of the 60 major fires. Figure 3 illustrates the estimates of total acreage burned per decade in the last 300 years.

Table 4.--Acreage of major fires on the HPP (scars from at least 5 trees).

Year	Size	Year	Size	Year	Size
1907	640	1841	1840	1788	1390
1881	2580	1839	250	1784	3090
1881	840	1838	1300	1782	1310
1879	2220	1835	270	1776	1460
1875	2650	1834	320	1776	290
1872	3710	1832	1020	1772	1740
1868	570	1826	1960	1769	1680
1866	3930	1824	530	1769	1560
1864	5870	1824	1550	1764	1640
1861	240	1821	1970	1751	1410
1860	1140	1820	2520	1742	3000
1860	1540	1817	1550	1730	1290
1859	1620	1817	1330	1729	1670
1856	1720	1812	2530	1723	2150
1856	1300	1809	860	1718	3470
1853	590	1808	1770	1706	2130
1846	230	1805	790	1692	2700
1844	800	1805	510	1679	3270
1843	2710	1803	2770	1676	2320
1841	630	1798	1600	1669	2100

Plateau subdivision incidence

Pre-settlement fire incidence values for plateau subdivisions parallel the sequence of values for the entire plateau. The decline in fires during the Grazing and NPS Periods is visible, albeit muted due to the prevalence of small, scattered burns in the last 50 years. From table 5 one can see that, for the portion of the pre-European Period where all recording trees were present (1801-1863), a fire occurred somewhere in a plateau subdivision every second or third year. The seemingly higher incidence of fire in the NPS Period, when compared to the Grazing Period, is misleading. As previously noted, fire records from the last thirty years have been incorporated along with the existing scar dates. Small fires prior to 1950 that did not result in scarring one of the sample trees are not represented in the incidence calculations.

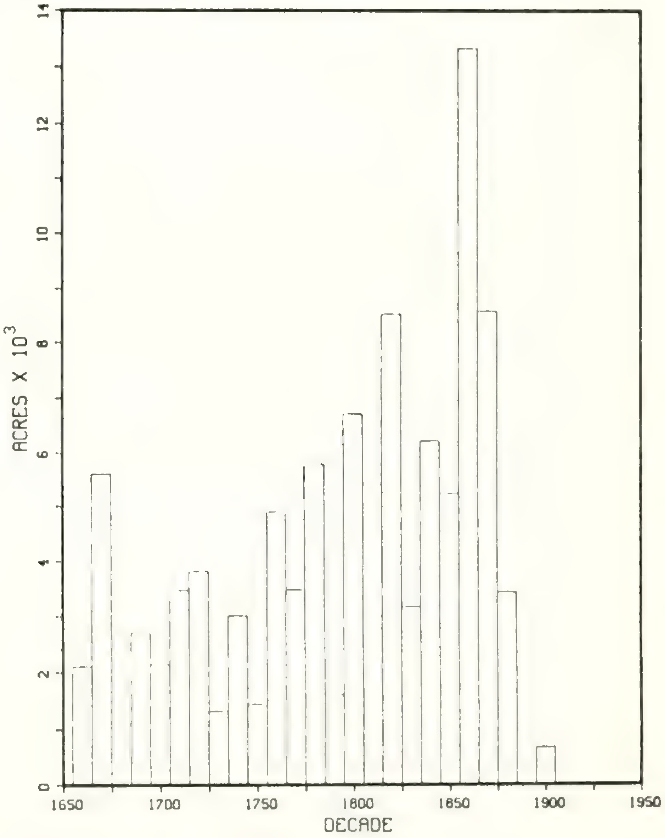

Figure 3.--Estimated amount of land burned per decade on the HPP

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[4] West, N. E. and W. L. Loope. 1977. Annual progress report to Zion National Park and USU-NPS Coop. Studies Unit regarding studies of frequency and role of fire in ecosystems of Zion National Park. Zion National Park, Springdale, Utah.

Table 5.--Fire incidence of HPP subdivisions (intervals between fires in years).

Unit	Time Periods				
	1751-1800	1801-1863	1864-1882	1883-1925	1926-1980
A	4.5	3.7	3.8	14.3	13.5
B	2.6	2.3	1.9	5.4	6.8
C	5.6	2.7	2.1	10.8	6.0
D	3.6	2.7	2.7	6.1	4.9
Mean	4.1	2.9	2.6	9.2	7.8

Table 6.--Fire incidence of HPP watersheds (intervals between fires in years).

Unit	Time Periods				
	1751-1800	1801-1863	1864-1882	1883-1925	1926-1980
1	8.3	7.0	9.5	43.0	27.0
2	7.1	7.9	3.8	43.0	54.0
3	25.0	7.9	9.5	43.0	54.0
4	7.1	7.9	4.8	21.5	27.0
5	4.2	4.8	4.8	21.5	--
6	3.6	7.9	4.8	14.3	18.0
7	7.1	6.3	3.8	14.3	18.0
8	8.3	4.2	4.8	21.5	27.0
9	12.5	4.8	2.7	10.8	7.7
10	7.1	7.0	4.8	21.5	13.5
11	10.0	4.2	6.3	43.0	54.0
12	5.0	4.2	3.8	10.8	27.0
Mean	8.8	6.2	5.3	25.7	--

Watershed incidence

Table 6 summarizes values for fire incidence organized by watershed. The small and scattered nature of modern fires is illustrated by the extremely variable range in the NPS Period; from none in Watershed 5 to every 7.7 years in Watershed 9. The latter watershed is the largest such unit and contains within it the spring and former cabin site at Potato Hollow. Heavy human usage by both ranchers and campers has probably contributed to the higher amount of fires there.

Fire Frequency

Grove frequency

Two groves were used to evaluate changes in fire frequency over the last 230 years. A striking similarity is visible between the Pre-European values for the two groves (table 7), despite separation by 9 km (5.5 miles). The 4 fires that occurred in Grove 2 during the Grazing Period were all apparently local, consuming less than 40 ha (100 ac). The larger size of Grove 2 increases the risk that certain of the fires recorded within its confines might not have extended throughout the entire grove. Thus, the values presented might, in some cases, be closer to incidence than frequency, as defined by Kilgore and Taylor (1979). Nevertheless, the values presented in table 7 are fairly close to the more definite frequency calculations of Grove 1.

Table 7.--Fire frequency of groves on the HPP (intervals between fires in years).

Unit	Acreage	N	Time Periods				
			1751-1800	1801-1863	1864-1882	1883-1925	1926-1980
1	30	7	8.3	7.0	6.3	--	--
2	100	8	8.3	4.2	6.3	10.7	54.0

Table 8.--Fire frequency from clusters on the HPP (intervals between fires in years).

Unit	N	Time Periods				
		1751-1800	1801-1863	1864-1882	1883-1925	1926-1980
1	4	25.0	21.0	9.5	43.0	--
2	2	25.0	15.8	9.5	--	--
3	2	25.0	12.6	6.3	43.0	--
4	3	25.0	31.5	19.0	43.0	--
5	3	12.5	12.6	6.3	--	--
6	4	12.5	12.6	9.5	--	--
7	2	16.7	15.8	19.0	--	--
8	2	16.7	15.8	9.5	21.5	--
9	3	12.5	6.3	19.0	--	--
10	4	25.0	15.8	4.8	43.0	--
11	2	50.0	9.0	19.0	--	--
12	2	--	9.0	19.0	43.0	54.0
13	5	10.0	5.3	6.3	14.3	--
Mean		--	12.0	12.1	--	--

Cluster frequency

Data from small clusters of two to five trees are shown in table 8. Clusters of two are only included if they have at least 10 different scar dates. While this may appear to be prejudicing the results, the inclusion of all clusters of two adjacent sampled trees, regardless of total number of scars, would have mingled inaccurate and misleading data with more accurate figures. Standards for accuracy for based on the examination of the composite scores for Groves 1 and 2. Most clusters not included above are located in the northern part of the HPP. Here the scarcity of older trees in the logged areas necessitated the sampling of trees with only a few individual scars.

Cluster fire frequency values are higher, indicating longer intervals between fires. Some of this is because certain fires did not burn an entire watershed or subdivision. Therefore, they are represented in incidence calculations but not in all possible cluster frequencies within a given unit. The small sample size of the clusters makes them err on the conservative side.

ndividual frequencies

Frequencies amongst individual trees varied remendously. There was a range from several ingle-scarred specimens (cut for practice or in reas with few potential samples) to one ponderosa ine with 20 scars. This exceptional tree rovided frequency values comparable with those of ne cluster data. In all, 22% of the sections at had more than five scars. Had an average een calculated based on the sum of all individual rees (even with only those with more than five cars), the results would have been extremely isleading, either on the plateau subdivision or ne watershed scale.

Church Mesa Chronology

The data obtained from the nine sample trees n Church Mesa gave intervals that contrasted ith those from the HPP. Four fires were ecorded--1757, 1813, 1892, and 1964. In addition ne NPS reached the mesa by helicopter in July, 976 to put out a small fire on a steep, east-acing slope covered by oak woodland. Whether his fire would have covered the entire mesa ithout human intervention is subject to conjecure. If it had, it would have departed dramaically from the pattern of the previous 200 years rom the scar dates, an average interval of 69 ears was obtained, with a range from 56 to 79 ears. Incidence approximates frequency on the 0 ha (370 ac) mesa, since nearly all of the mple trees show the same dates. Human activity s had essentially no impact (until the recent S fire control effort), so the historical time riods used on the plateau are irrelevant. wever, two of the four fires recorded from urch Mesa in the last 225 years occurred after e sharp decline in fires on the HPP in 1882. thropogenic phenomenon, rather than climatic ifts are thus implicated.

A marked difference in vegetation structure s observed on the mesa. In contrast to the nse shrub and sapling strata found throughout e forests of the plateau, a uniform groundlayer grasses dominated under widely spaced ponderosa ne on Church Mesa. Oak woodlands were also fferent from the plateau, and often featured patchier structure with grass-dominated interaces (Madany 1981).

Age-Class Relationships

e at first scar

Sixty-seven of the 123 sample sections conined the pith and could be used to calculate e age at which a tree was first scarred. Sixtyur of the trees were ponderosa pine with the mainder including one each of white fir, uglas fir, and Rocky Mountain juniper. gure 4 illustrates the range in values for nderosa pine. The period when a pine is most susceptible to scarring seems to be between the ages of 10 and 80. Scars can still be initiated after the tree has reached great age and girth. Probably few pines survive fires when they are less than 10 years old unless the immediate fuel load is scanty and/or moist. Thus, at the pre-European frequencies displayed above, regeneration density could have been largely controlled by fire. Trees that survived their first 10 years were either those in patches of land that escaped burning or places with little fuel accumulation. The three values for the non-pine sections are all at or below the mean age for ponderosa pine.

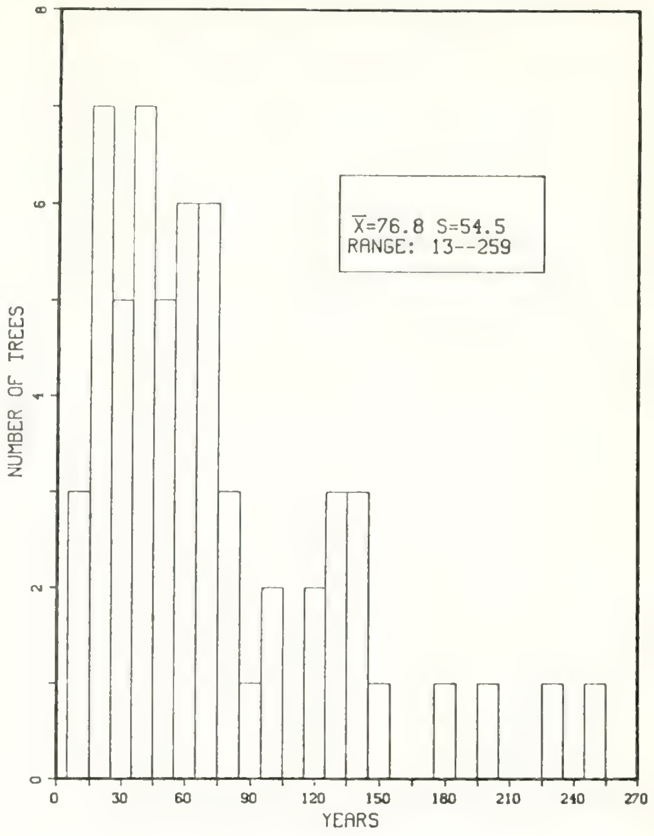

Figure 4. Age at the first scar from 64 ponderosa pine.

Age-size class distribution

Dates from increment cores taken from 134 trees at the 95 vegetation sampling plots on the HPP support the conclusions based on the fire scar record. All major tree species (ponderosa pine, Gambel oak, Rocky Mountain juniper) show a dramatic increase in the early years of this century following the cessation of burning. Ponderosa pine and juniper establishment was greatest in the 1920's, while Gambel oak numbers peak around 1900 (Madany 1981).

CONCLUSION

The incidence of large wildfires on the HPP decreased markedly at a point in history when great ecological changes were taking place (Madany 1981). The introduction of large numbers of livestock resulted in overgrazed conditions at least as early as the 1890's. The range was described as fully stocked by 1875.[5] Between these two dates, fires declined sharply. This gives strong circumstantial evidence that the reduction of grass from the pine and oak savannas eliminated a critical fuel component (Madany 1981). Subsequent shifts in vegetation structure (i.e., the formation of the dense understory of saplings and shrubs) solidified the initial change. A new fuel environment prevailed in which fires could not burn as readily. As grazing was phased out, the NPS began its fire suppression activity and successfully prevented any major conflagrations from occurring. However, in June of 1980, a camper-ignited blaze consumed 65 ha (160 ac). This was not only the largest fire since 1907, but was probably the most severe fire the 200 to 600 year old ponderosa pines it killed had experienced. Thus, land use changes, especially grazing, have drastically altered the fire regime from frequent, light surface fires to infrequent, severe crown fires. Without further human intervention, a return to either pristine vegetation or fire regime is probably impossible on the HPP.

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The Use of Land Survey Records in Estimating Presettlement Fire Frequency[1]

Craig G. Lorimer[2]

Abstract.--Records from early government land surveys can be used to estimate the proportion of stands killed by fire in a 15-25 yr period preceding the survey for vast areas of presettlement forest. Identification of post-fire stands is possible in some regions. Assumptions and problems of interpretation are discussed.

The determination of natural fire frequency in many of the forest types of eastern North America is beset with difficult problems. Some of the standard techniques of fire history analysis that are so useful in the West have only limited application in the East. Virgin forest remnants are so rare in most areas that opportunities for on-site research are geographically very limited in scope. These analyses generally must rely on a limited number of increment cores rather than stem cross-sections, and the record of disturbance seldom extends further back than 350 years, the usual maximum lifespan in most species. Moreover, trees of many species are easily killed by moderate or severe fires, or even smoldering ground fires in duff. Especially in hardwoods, any fire scars that do form are often obscured by decay, obliterating valuable information.

An alternative approach that is potentially useful for analysis of fire history over large areas in the East is the study of early government land survey records. This paper will focus on the methodology, with particular emphasis on the underlying requirements and assumptions for valid interpretation. Examples will be drawn largely from surveys in the hemlock-northern hardwood and spruce-northern hardwood region extending from Wisconsin to Maine, which seems to be particularly suited to the method. Possibly it will be found useful in some other parts of the country as well.

NATURE OF THE DATA

The primary purpose of the surveys was to establish boundaries for a grid of square townships. But the field books contain systematic descriptions of many natural features including forest species composition, recorded in order that the supervisors of the survey could judge the relative value of each township for farming and timber production (see Bourdo 1956 for full documentation). Surveyors were required to describe the species of trees along each mile of township line in order of their predominance, and in most surveys, the species and diameters of 4 "witness trees" facing each section corner were recorded. Of even greater interest to fire ecologists is that the surveyors recorded the extent of burned lands and windfalls that intercepted the township lines. It was not uncommon for surveyors to encounter burned land, or even forests actually on fire. There seems little doubt that this record of burned land was made consistently. Virtually every mile of survey has a forest description, and it is unlikely that a surveyor would pass through a mile of burned land and simply record the species as if the trees were alive. The notes, in fact, are sufficiently complete that it is possible to map the boundaries of the large burns solely from the field notes (fig. 1). The surveys thus provide a "snapshot" of the fire-mosaic over a vast area at a given point in time. From this information, the average recurrence interval of moderate and severe fires can be calculated for the region.

Light surface fires are ordinarily excluded from this type of analysis. We can probably assume that any fire that did not cause heavy mortality of overstory trees remained unrecorded unless it occurred within a year or two before the survey.

ANALYSIS OF RECENT BURNS

One approach in estimating fire frequency simply involves a tally of the total area of "recently" burned forest and an estimate of the time span over which these fires occurred. For large burns, area can be estimated by dot grid, but if small burns are numerous, area is best calculated by formulas designed for line-transect samples (Canham 1978).

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[1] Paper presented at the Fire History Workshop, Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980.

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The question of how long an area would be recognized by the surveyors as being burned land must be considered. This could well vary among surveys; in Maine the area of the great fire of 1803 was repeatedly called "old burnt land" by all 3 surveyors who traversed the area in 1825 and 1827. The fire origin was recognized by the small paper birch (Betula papyrifera) and aspen (Populus tremuloides and P. grandidentata), "all of a second growth ... not exceeding 4 inches in diameter," and probably by standing snags as well. Most surveyors would probably call an area "burnt land" during the entire "brushy" period prior to canopy closure, which on most sites in the region would occur about 15 years after fire (fig. 2). In the Wisconsin survey, statements such as "burnt pine grown up with aspen brush" are common.

The analysis of recent burns is probably feasible in many closed-canopy forest types, but its main limitation is that the time span involved, such as 15 years, is a rather narrow time interval on which to base fire frequency estimates. If the interval includes an unusually severe fire year, it may cause overestimation of long-range fire frequency, and the opposite situation may cause underestimation. The northern Maine survey (Lorimer 1977) included the notorious year 1825, probably the worst fire year in the region in recorded history. However, since the land surveys of some states took nearly 100 years to complete, this can lessen the problem somewhat by extending the time base.

INTERPRETATION OF STANDING FORESTS

This time base for the fire frequency estimate can be considerably extended if we can dependably recognize seral, post-fire forests from the surveyors' lists of principal species. The restrictions on the approach, however, are important and should be carefully examined. Successional patterns in the region must be distinctive and consistent. The seral types must be so nearly dependent on fire that any stands of these species can safely be assumed to be of fire origin, and the seed source must be so nearly ubiquitous that burned areas would rarely go uncolonized by pioneer species. Likewise, the climax species must be somewhat poorly adapted to invading burned land, and those seedlings that do become established would not successfully compete with pioneer species for overstory dominance.

Are there forest types in which these stringent requirements can be met? A preliminary evaluation for northern Maine suggested that the paper birch-aspen type, which is common throughout the Northeast, qualifies as such a diagnostic element of fire in the upland forests of red spru (Picea rubens) and northern hardwoods. Although scattered paper birch may become established on windfalls, stands heavily dominated by paper birc and aspen rarely occur except after fire. This dependable relationship was noted by Dana (1909), who remarked "So intimate is this relation betwee paper birch and cleared or burned-over land that it is fairly safe to assume that areas containing a good stand of birch have either been burned or

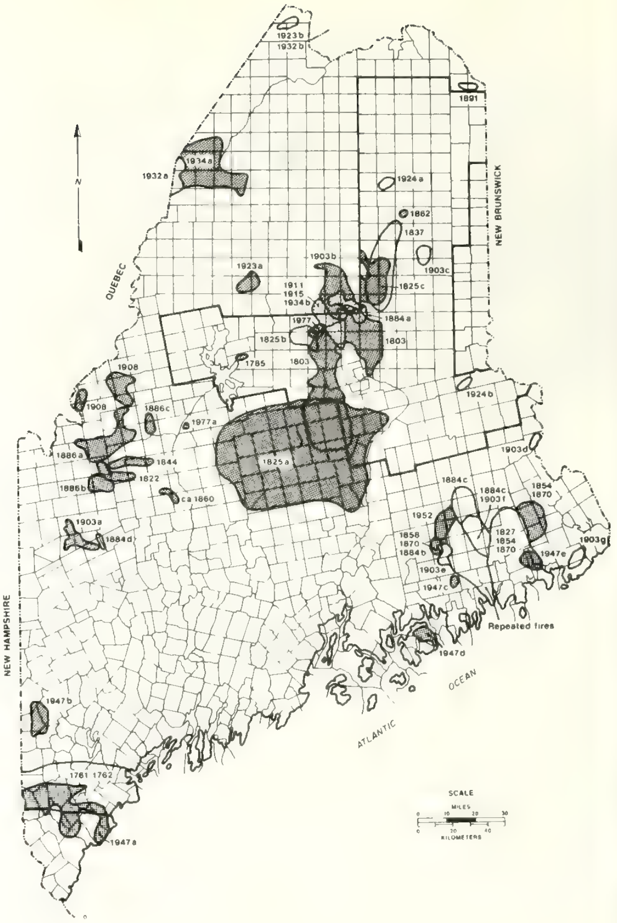

Figure 1.--Coolidge's (1963) map of major recorde forest fires in Maine, revised to incorporat information from land survey records and other sources. Information on post-fire species composition, and fuel and weather conditions, was derived from the following sources: Morse 1819, Land survey records of 1797-1827, Cary 1894, 1896, Spring 1904, Dana 1909, records of the St. Regis and Grea Northern Paper Companies, John Sinclair, 7 Islands Land Co., foresters with the Maine Forest Service, and personal reconnaissance. Burned areas for which information on post-fire regeneration is available are indicated by stippling. Presettlement fire frequency estimate is based on the study area enclosed by dark lines.

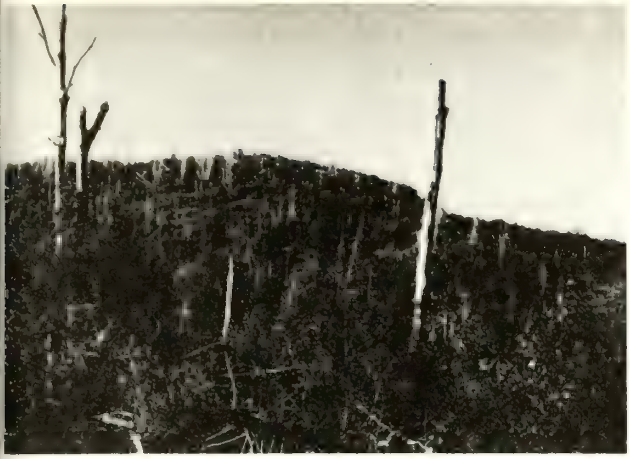

Figure 2.--Aspen, paper birch, and pin cherry 11 years after crown fire in a spruce-northern hardwood forest, near St. Andrews, New Brunswick.

previously cultivated." It thrives on nearly all sites except the wetter bogs and the drier sand plains. The seeds are very lightweight and may be borne by wind for long distances, and large numbers are produced almost every year (Fowells 1965). This accounts for its "sudden appearance in dense stands on burned or cut-over areas even when there is not a single seed tree in the immediate vicinity" (Dana 1909).

It is not unusual for spruce and other tolerant species to appear within a few years after a fire, but they quickly lapse into the understory because of their slower growth (fig. 3). After 50-60 years the spruce may penetrate the overstory, forming a mixed stand. Decadence of the birch and aspen begins after about age 75-80, although a substantial number of individuals will often persist to ages 95-110 (Cary 1896, Weigle and Frothingham 1911).

The critical assumption that the "climax species" rarely dominate a burned area needs careful documentation. In Maine, all the major historic fires for which evidence was available (fig. 1) had regenerated almost entirely to birch-aspen despite a wide range of burning conditions and seed source availability. Soil conditions ranged from stony loams to coarse gravels and sands. Some fires were "flashy" spring fires (e.g. 1903, 1934a), and others were deep-burning fires in summer (1952, 1977b) or fall (1825a, c, 1947). Some were principally crown fires in mature coniferous timber (1934a, 1947c, d, e), or in young conifers (1903e, 1952); others burned in areas with numerous windfalls (1803, 1825a, 1977b). The largest number of fires occurred in slash after logging or land clearing (1822, 1825a, 1884a, 1886, 1903a, b, 1911, 1923a, 1947a). Some of the fires, notably those of 1785 and 1803, occurred at a time when paper birch and aspen seed trees were found in very low densities,

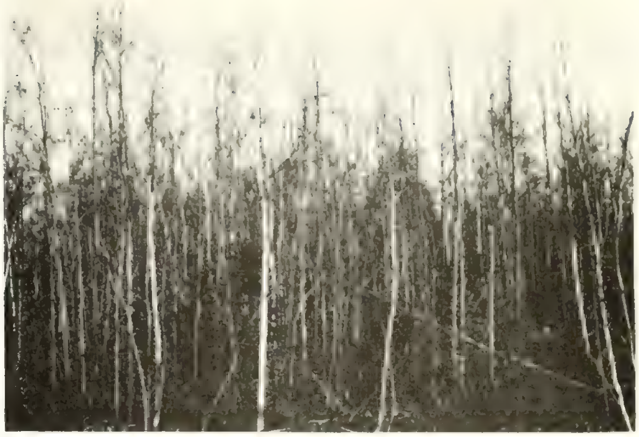

Figure 3.--Growth of aspen and birch 27 years after the fire of August 1952 in eastern Maine. The scattered spruce in the understory are nearly as old as the aspen, but have lagged behind because of slower growth. This fire burned largely in young immature spruce stands.

averaging less than 5% of the total tree density (1825 land survey data). Fires in hardwood stands are relatively uncommon, but several areas of fire-killed northern hardwoods that regenerated to birch-aspen can be documented. Recent examples are portions of the 1934a, 1952, and 1977a burns. The most notable example is the fire of 1825c, for which surveyors made reference to 25 km of "hardwood killed by fire" along township lines. The area is shown as merchantable paper birch on Dana's (1909) map. Westveld (1939) likewise noted that fire-killed northern hardwoods generally revert to paper birch and aspen if mineral soil is exposed.

A few small parts of the 1803 burn did not regenerate to birch-aspen. One mile of township line was described as "formerly pine forest, burnt totally about 20 years ago. Thick growth of small spruces has succeeded." Exceptions to the usual pattern may occur occasionally if seed distribution is erratic or if a crown fire leaves the surface of the ground largely unburned. Such exceptions must be viewed as a source of error in the method, although in northern Maine it does not appear to be a serious problem.

This successional pattern appears to be common in much of the Northeast and Lake States. Of particular interest is the report of Hosmer and Bruce (1901), showing birch-aspen colonization of several burns < 30 ha in size in the spruce region of the Adirondack Mountains, New York, even though seed trees were uncommon on the township. However, it is not known if exceptions to this successional pattern are common in these areas, and more detailed studies will be needed. The recognition of post-fire forests in the Northeast and Lake States may also be restricted if some surveyors did not consistently distinguish between paper birch and yellow birch (Betula lutea), since the latter is not a reliable indicator of previous fire. Much of the "green timber" reported in the Wisconsin survey cannot be analyzed for this reason.

SCALE OF FIRES REPORTED

An important methodological question concerns the size of the burned areas reported. Would small burns intercepting only a fractional part of a surveyed mile go unreported, and might not the cumulative effect of this under-representation have a major effect on calculated fire frequency? In the survey notes, however, it is common for burned areas to be reported along distances as short as 0.4 km. A circular area of such dimensions covers only 13 ha, so it can be seen that fairly small burned areas were reported by surveyors.

Evidence on older burns of small to medium size (20-150 ha) can be obtained in some cases from a tabulation of species of witness trees. If small intense fires were common and had a major influence on forest composition, we might expect a reasonable proportion of witness trees of seral species in the green standing timber outside the areas formally recognized as burned land, provided that successional patterns are similar after fires of this size range. This could be a useful analysis in some parts of the country, especially where trees of seral species are long-lived. In the Northeast it may be less useful because paper birch and aspen in older stands may have been avoided for witness trees because of the poor risk. For post-fire stands less than about 50 years old, however, the surveyors in most cases would have had no other alternative but to use paper birch or aspen, as in the stand shown in figure 3. In Maine the proportion of witness trees of these species in the green standing timber was quite low (3.0% and 0.3%, respectively), and some of these may have germinated on windfalls rather than burned land. This line of evidence does not seem to support a major role for fires of this size range in northern Maine, but in regions where this is not the case, approximate correction factors for fire frequency estimates could perhaps be derived from the witness tree counts.

FIRE FREQUENCY IN THE NORTHEAST: PRELIMINARY FINDINGS

Analysis of the northeastern Maine land survey data indicated that 3.9% of the landscape had been recently burned (within about 15 years of the survey), mostly in 1825; 5.1% was young birch-aspen forest, mostly from the fire of 1803; and only 0.6% of the area had older paper birch and aspen, either alone or mixed with other species. The lack of extensive areas of mature birch-aspen implies that no fires of great size occurred between 1750 and 1800, an inference that is consistent with the low incidence of charcoal in lake sediments prior to the 19th century.[3] It is possible, however, that smaller areas of mature birch-aspen were not recorded or occurred as mixed stands that might not always be apparent from the surveyors' descriptions.

The apparent fire frequency indicated by the mosaic of burns for this time period is rather low despite the three extensive fires. Even the shorter 15-yr interval that included the severe 1825 season yields a calculated recurrence interval of about 400 years for moderate or severe fire in a given stand of trees, while the entire 75-yr interval (1750-1825) yields an estimate of about 800 years. There may be considerable temporal variability among successive time intervals, although the inclusion of an unusually severe fire year makes it less likely that the fire frequency from 1750-1825 was abnormally low. In fact the proportion of total area burned by large fires during this interval actually exceeded the proportion burned during the subsequent logging era of 1835-1910, which also included a severe fire year (1903). By comparison, the calculated recurrence interval for the 20th century, based on fire reports for fires of all intensities, is 260 years for the period 1903-1912 and 710 years for the period 1913-1960 (Coolidge 1963).

Evidence from other areas is still fragmentary, but apparently few areas of fire-killed timber were present at the time of the land surveys in parts of New York (McIntosh 1962), Vermont (Siccama 1971), and Pennsylvania (Lutz 1930). Hosmer and Bruce (1901), in a detailed investigation of a township of virgin spruce in the Adirondacks, reported that only 1% of the township was occupied by burns up to 50 years old, suggesting a surprisingly low fire frequency.

A generally low fire frequency in sizable areas of the Northeast seems to be indicated by other evidence independent of the land surveys. Many of the early foresters who were aware of the fire situation before the advent of organized fire suppression stressed the low fire hazard in standing green timber, even for the spruce-fir type in severe fire weather. Ayres (1909) stated that for northern New Hampshire "fire seldom sweeps through virgin forest; the slash left by lumbering is a chief promoting cause of fire, and it is in the slash that nearly all fires originate. A map of the fires in the White Mountain region shows that they have closely followed the cut-over areas." Similar statements were made by Spring (1904) and Chittenden (1905), although some cases of slash fires sweeping into virgin timber were noted. Even in the extremely severe season of 1903, Spring (1904) noted that "in not a single case over the entire area in this region did the fire penetrate into a virgin stand for more than 10 rods." Some large fires would surely occur in the absence of man, but they do not appear to have been frequent except in windfalls and other concentrations of dead trees.

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[3] Swain, Albert M. 1980. Unpublished data on file, Center for Climatic Research, University of Wisconsin-Madison.

Even more important evidence deals with the age structures of virgin stands. If the recurrence interval of severe fire were less than 300 years, most virgin stands should have been even-aged or nearly so. Yet most remnants that have been studied, from Wisconsin to New Hampshire, were broadly uneven-aged or all-aged (e.g. Zon and Scholz 1929, Gates and Nichols 1930, Westveld 1933, Hough and Forbes 1943, Leak 1975). This concurs with the opinions of early foresters who were able to examine logging operations in virgin forests of the Northeast (Graves 1899, Hawley and Hawes 1912, Dana 1930). Hawley and Hawes (1912) noted that "exceptions to this [uneven-aged] character occur; for sometimes a part of the forest is found where the trees are all of one age over considerable areas . . . but such cases are in the minority." Even if fires causing heavy tree mortality recurred on most sites only once in 500 years on the average, at least 40% of the landscape should have had even-aged stands (up to 200 years old) of fire origin alone, without even taking into account those resulting from windthrow and insect infestations.

A broader perspective on fire frequency in the Northeast and Lake States will develop as additional evidence is obtained. Undoubtedly there is much variation within a region due to vegetative, soil, topographic, and climatic differences. The pattern of burns in figure 1, for example, reveals at least two areas of relatively high fire hazard that have been burned repeatedly. Perhaps the land survey records will be of further use in analyzing regional variations. Approaches other than land survey analysis, such as the study of charcoal in lake sediments, will be needed to provide evidence on the frequency of lower intensity fires and smaller fires.

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Fire History and Man-Induced Fire Problems in Subtropical South Florida[1]

Dale L. Taylor[2]

Abstract.--Historic fires, indicated by charcoal deposits, endemic plants, and lightning-caused fires, probably occurred during drought cycles of about 8 years, were several thousand acres in extent, and probably burned most of the fire-adapted vegetation every two cycles.

Environmental perturbation has created a critical fire situation with extreme years occurring at 5.8 to 7.5 year intervals, and moderate years at 3.2 to 4.3 year intervals.

INTRODUCTION

South Florida is an area with a high number of fires, but also where fire intensity, fire frequency, and fire type may be changing. Benign wet season fires now rarely occur, being replaced by man-caused and man-induced dry season fires that may burn more frequently and burn larger areas. Newly established exotics, such as the cajaput (*Melaleuca quinquenervia*), may permit crown fire for the first time, whereas *Schinus terebinthifolius*, forms a low, but dense, fire retardant forest.

Two areas in south Florida which this paper is concerned with are the 1.4 million acre Everglades National Park, established in 1947, and the 570,000 acre Big Cypress National Preserve established in 1974 (fig. 1). These two areas may be the most fire prone units within the National Park Service system. The 1948-1979 Everglades National Park fire records contain 682 fire reports that cover 451,082 burned acres. The first 21 months of Big Cypress fire records show that 131 reported fires have burned 40,370 acres. Both parks have been disturbed by drainage, lumbering, farming, off-road vehicle use (Big Cypress), and invasion by exotic plant species. Other federal and state lands also have extensive fire problems (fig. 1).

The climate in south Florida is subtropical with alternating wet and dry seasons. Rainfall for 1979 totaled 51.7 inches in Big Cypress and 52.8 inches at Royal Palm in Everglades National Park, but wide annual fluctuations between 30 and 100 inches may occur (Leach et al. 1972). June to October is the wet season when water covers the soil of most community types, except hammocks and pinelands, and when most cloud-to-ground lightning occurs. November into May is the dry season, and the time when most man-caused fires occur.

Wade et al. (1980) describe fire impact on the diverse mosaic of at least 10 major vegetation types: sawgrass; wet prairie and slough; marsh and marl prairie; saltmarsh; pine flatwoods; Miami rock ridge pineland; tree islands and hammocks; cypress; mixed-hardwood swamps; and mangrove. Long (1974) has concluded that the south Florida flora is the youngest flora in North America, about 3,000 to 5,000 years old at most, and therefore one of the most modern floras known. Because of its youth many niches may not be filled, allowing exotic vegetation to become established (Wade in press). The pinelands may be much older than suggested by Long, as Robertson et al. (1974) feel the Miami Rock Ridge, the Florida Keys, and other high spots may have persisted as islands through interglacial periods.

The following evidence strongly suggests that natural fire has been a constant factor affecting the local distribution of vegetation types, and that arrangement of plant cover types probably has been similar to that seen today.

Pre-aboriginal Period

Charcoal deposits

Studies of peat soils indicate they could have accumulated only in a wet, boggy environment beginning about 5500 years ago (Parker 1974).

Peats from the Everglades and coastal swamps of southern Florida contain numerous charcoal-rich lenses which represent ancient fires (Cohen 1974, Parker 1974). Peat from sawgrass (*Cladium jamaicensis*), and *Acrostrichum-Cladium* peats tended to have consistently high charcoal contents compared to mangrove (*Rhizophora*, *Rhizophora-Avicennia*) peat, *Conocarpus* (buttonwood) peat, or bay hammocks (*Myrica-Persea-Salix*) peat. Cohen (1974) felt that the inability to find charcoal layers at the same levels in any cores indicated fires, although common, were probably restricted to environments with the greatest fire potential. He concluded there was no evidence to support the contention that there ever have been prolonged dry periods which resulted in widespread burning of peat (and resultant widespread, observable charcoal layers) in the Everglades. Parker (1974), on the other hand, stated that there were times of alternating drought and flood, with some droughts of several years duration when fires in the glades ravaged the vegetation and burned the organic soils to the water table, producing ash layers several inches thick.

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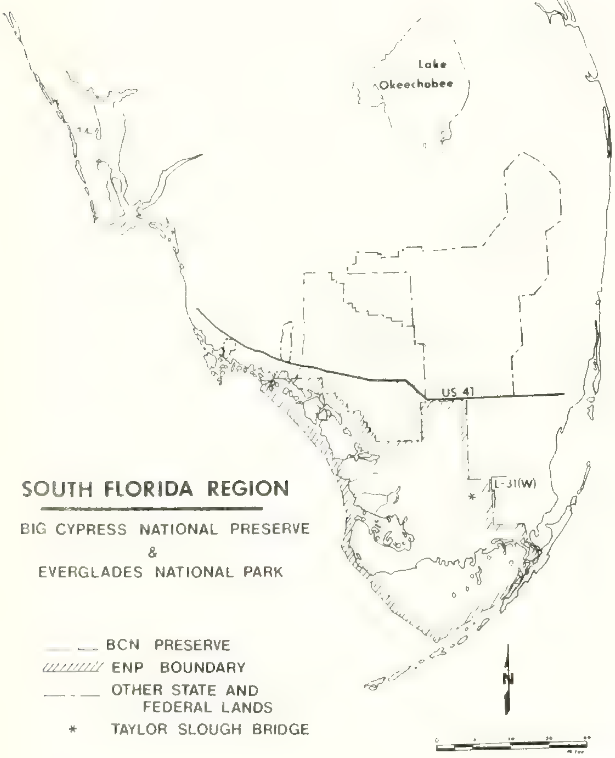

Figure 1. The south Florida region is the area south of Lake Okeechobee. Two National Park Service units, the Big Cypress National Preserve and Everglades National Park make up a large part of the region. Note the location of canal L-31(W) and Taylor Slough Bridge.

Endemic plants

Avery and Loope (1980) list 65 plant taxa as being endemic to south Florida. Well over half are limited to pine forests and 70% are herbs or low shrub plants maintained by fire (Robertson 1953). Robertson (1953) states that evolution of these low-growing plants required that their sub-climax habitats exist for a long period of time, and this in turn required recurring natural fire. Almost all endemic and other low shrub and herbaceous plants are shaded out by hardwoods invading pine forests that are fire free for as little as five years (Robertson 1953). Robertson concluded that their existence as distinct species is inescapable proof of regularly recurring natural fire sufficient to maintain large areas of sub-climax vegetation. Pine islands may have persisted through interglacial periods (Robertson et al. 1974) allowing plant evolution to continue for long periods. In contrast Long (1974) states that the existence of the south Florida flora is striking proof of the relatively short time required for the evolution of highly complex ecosystems. He concludes the presence of numerous endemic species and subspecies, plants found nowhere else in the world, may also constitute circumstantial evidence that highly specialized organisms can evolve in far less time than has been postulated for the development of new forms.

Lightning

The assumption by early authorities that natural fires were too infrequent to be of consequence hindered understanding of the role of fire in south Florida (Robertson 1953). Not until 1951, when lightning-caused fires were observed from a fire tower, was the role of lightning understood. It is now reasonable to assume lightning fires have been a factor throughout the geological existence of the region and that fire-maintained cover types have been a constant feature of the south Florida vegetation (Robertson 1953).

Florida has 70 to 90 thunderstorm days per year, more than any other place in the nation (Maier 1977). Most cloud-to-ground lightning strikes occur from June through September (Taylor and Maier unpublished data). Tentative data show probable mean annual ground flash density varies from 4 to 12 flashes per km^2 (fig. 2). Fewer strikes occur in Everglades National Park compared to the Big Cypress National Preserve (fig. 2), but for unknown reasons more lightning fires occur in Everglades than occur in Big Cypress.

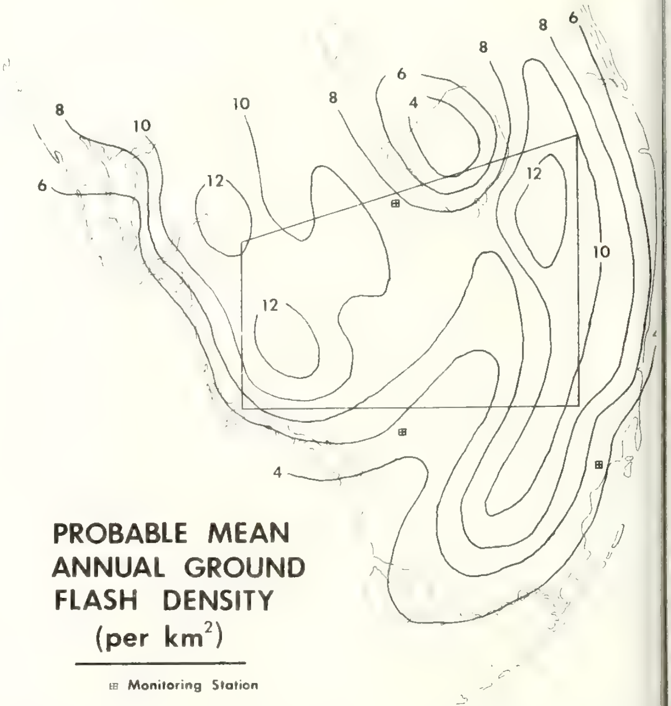

Figure 2. Probable mean annual ground flash density for cloud-to-ground lightning in south Florida. The trapazoid represents the primary target area in the National Oceanic and Atmospheric Administration lightning monitoring experiment (Taylor and Maier, unpublished data).

The lightning fire season is May through August when 87% of all lightning-caused fires occur, but lightning fires have been recorded for all months except January and February (Taylor in press). June is when most acreage burns and when the largest lightning-caused fires occur. In Everglades National Park lightning fires account for 28% of all fires and 18% of the acreage burned. An average 2540 acres will burn due to lightning ignition each year. An exceptional year was 1951 when nine lightning-caused fires burned 43,155 acres which constitutes 53% of the acreage burned due to lightning, and 10% of all acreage burned. The 1951 wet season was late in arriving and water levels were still low in June, creating an exceptional fire year in modern records. Such conditions may have been the rule in pre-man times when lightning was the major ignition source.

Aboriginal Period

Griffin (1974) states that the earliest dated archeological materials are from B.P. 3400 ± 100 or 1400 B.C. This places Indians in south Florida a few hundred years after the flora became established. Robertson (1954) did not see the need to invoke Indian fires as a major factor in the origin of fire maintained vegetation types. He felt natural fires must have been sufficiently frequent from earliest times to maintain large areas of sub-climax vegetation.

Indian use of fire may have been careless and the wildfires they caused probably were frequent. This addition of Indian fires to recurring natural fires must have caused fire incidence to increase sharply as Indians became established.

Post-settlement Fires

When white people first arrived in south Florida, they found Indians using fire for a variety of purposes, and they quickly adopted the practices themselves (Wade et al. 1980). Robertson (1953) believed the frequency of fires increased sharply as whites replaced aborigines in the area. Fires set accidentally as a result of farming or lumbering operations, and from incendiary activities, create an imposing picture of fire occurrence for the period of European settlement in south Florida (Robertson 1953). Incendiary fires were set to kill mosquitoes and rattlesnakes, clear brush, drive game, and to create fresh pasture for cattle or deer. Burning to locate gator holes in sawgrass was a common practice of commercial hide hunters.

As European whites became established, drainage of the everglades began. With the lowering of water levels the greater frequency of fires caused increasingly severe damage by consuming organic soils and destroying hardwood vegetation (Robertson 1954). Water levels were lowered by local drainage at various points, and by cutting off north to south water flow from Lake Okeechobee. Drainage was partially effective by about 1918 (Robertson 1954). Parker (1974) used the 1940-1946 hydrologic conditions as those most representative of the pre-drainage period. Data obtained since 1948 were felt to be unduly influenced by huge drainage projects, pumping and storage works, and by explosive urbanization.

Man-caused fires accounted for 36% of all fires and 62% of the acreage burned from 1948 through 1979 in Everglades National Park (Taylor in press), but in Big Cypress National Preserve, man-caused fires made up 89% of the total fires, 89% of the acreage burned and 99% of the suppression cost for 1979 (Taylor 1980). Man-caused fires may occur every month of the year but fires during July through September are of little consequence.

The man-caused fire season is from November through May, with January through May being months when most fires occur. The largest average fire size and the most acreage burned is by man-caused fires during May.

There is a low correlation between the number of park visitors and the number of man-caused fires (coefficient of -.273 on number of fires and -.034 on number of acres burned). The fire records suggest that those who set fires fit the pattern of woods burners described by Doolittle and Lightsey (1979). They found active woods burners in southern states to be young, white males whose activities are supported by their peers. An older, less active group has probably retired from active participation but act as patriarchs of the burning community.

Fire Season

Two fire seasons have been documented for south Florida: (1) The summer wet season (May through August) when fires are caused by lightning; and, (2) the winter dry season (November into May) when man-caused fires occur. Winter dry season fires include 246 known prescribed management fires that have burned 89,167 acres in Everglades National Park (Taylor in press). Most prescribed fires (88%) have been set from October through April, burning 95% of the acreage burned by prescribed fire (fig. 3).

If Everglades National Park and Big Cypress National Preserve were in strict adherence to National Park Service policies (NPS-18), all man-caused fires would be aggressively attacked, a formidable task.

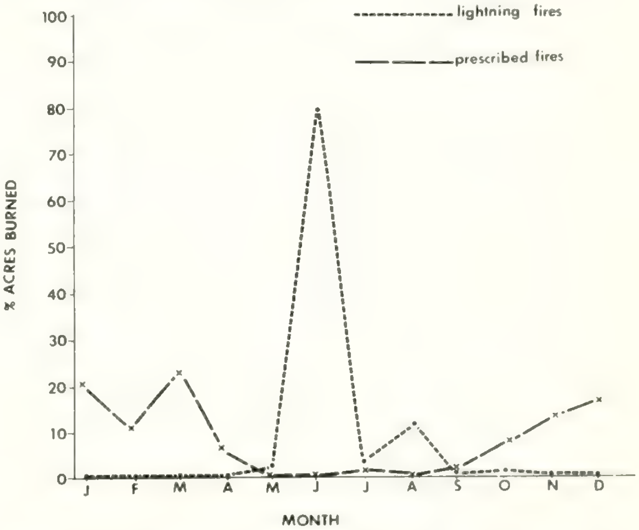

Figure 3. Monthly distribution of acres burned by prescribed fire and lightning-caused fire (from Taylor in press).

Some man-caused fires are allowed to burn if they meet a previously defined prescription in the approved Everglades National Park Fire Management Plan (1979). Many fires in Big Cypress burn out before they are discovered, but all others are manned at high expense.

Service policies require prescribed management fires to simulate, to the fullest extent, the influence of natural fires on the ecosystem. Prescribed management fires and natural lightning fires are out of sequence in Everglades National Park (fig. 3). Attempts now being made to conduct prescribed burns during the summer wet season have been successful, and a research program to evaluate summer versus winter season fires has been instituted (Taylor 1980).

Fire Frequency

Subtropical south Florida ecosystems do not permit fire frequency documentation as described by Arno and Sneck (1974). Graminoid communities recover quickly following fire, and they leave little evidence to show they were burned. Only three tree species that form annual rings, the south Florida slash pine (Pinus elliottii var. densa) and cypress (Taxodium distichum and T. ascendens) (Tomlinson and Craighead 1972), are sufficiently widespread to be useful for fire history documentation. However, bald cypress (T. distichum) trees usually are killed when organic soils are burned out, and any fire record disappears with the trees. Dwarf pond cypress (T. ascendens), present in cypress prairies, show fire scars and they may reveal fire frequency for one community type. Their slow growth, however, will make interpretation of rings difficult.

Slash pines are not useful for documenting fire history in Everglades National Park because the forests were cut-over about 1940. Some virgin pines do remain in Big Cypress, and many are fire scarred, but contrary to Tomlinson and Craighead (1972), we question whether the rings represent annual growth increments. Our reasons are as follows: (1) Langdon (1963) reported diameter growth throughout the year in slash pine growing on sandy soils on the west coast of Florida. (2) Ongoing studies of trees growing on limestone rock on the east coast show growth can occur every month of the year, depending upon the year (Taylor unpublished data). (3) In addition, an attempt to correlate fire scars on a tree cut July 28, 1979 with known fires in 1975, 1972, and 1968, proved erroneous for two of the three years.

Lacking biological documentation for fire frequency, fire records were used. Robertson (1953) pointed out south Florida is unique in that it has had more fires and kept less account of them than any other sector of the country, consequently, the study was limited to Everglades National Park fire records (Taylor in press).

Fire frequency was estimated by attempting to determine periods between extreme fire years and periods between moderate fire years. An extreme fire year was defined as a year when, before fire records, fire conditions received considerable discussion in the popular press, or when fire records showed unusually large numbers of fires and/or acres burned.

Frequency between extreme fire years was estimated from several sources. (1) A list of extreme years from 1910 to 1953 was gleaned from newspaper accounts (Robertson 1953); (2) The total number of acres burned each year in Everglades National Park from 1948 through 1979 (Taylor in press); (3) The number of fires that burned each year in Everglades National Park from 1948 through 1979 (Taylor in press); (4) A regression equation, based on the relationship of man-caused fires to water levels and precipitation, was used to estimate number of fires from 1933 through 1947 (Taylor in press); (5) By counting the number of years when the annual mean acreage burned by man-caused fires, and the annual mean total acres burned exceeded the five-year mean that had exceeded the mean for the period of record (fig. 4). These methods resulted in an estimated 5.8 to 7.5 years between extreme fire years.

Moderate fire frequency was estimated by counting the number of years when total acres burned exceeded the mean for the period of record. A moderate fire season will occur every 3.2 years if total acres are used in the calculations, or 4.3 years if only number of man-caused fires is used. Moderate fire frequency estimated from total acres burned is higher due to the influence of prescribed management fires.

William B. Robertson, Jr. and this author contend that historic natural fires were lightning-caused, occurred during the summer months, and burned several thousand acres during drought intervals of about eight years. Some droughts would have been more severe than others, and not all areas would have burned every interval. Few areas would have escaped two cycles in succession, however.

Today most lightning caused fires have little chance to spread because of roads, canals, and artificially high water levels maintained in Shark Slough during the dry season. The annual average of 2540 acres burned by lightning caused fire would result in a burning cycle of more than 200 years for the burnable parts of Everglades National Park. This is too low a level for fire dependent plants to evolve under, consequently, large lightning-caused fires must have been the rule in historic times.

The Future

There is little question that fire frequency has increased with the advent of Indians and white man, but the era of the Indian is over. The impact since European settlement will continue, and with increased drainage, urbanization, and further spread of exotics, fire frequency and fire severity will increase.

Drainage and subsequent shortening of the hydroperiod probably have influenced fire even during normal years. Longer periods with reduced water levels would allow more fires to occur at the transition from dry to wet, or wet to dry seasons (Taylor in press). As an example of water level change, Rose et al. (in press) report the highest water level at Taylor Slough bridge was during October before construction of canal L-31(W) (fig. 1). After canal construction highest water level was a month earlier, with October and November levels showing a decrease of 0.58 and 0.69 feet respectively. The greatest overall decrease occurred during June when mean surface water levels decreased by 1.03 feet, a decline of 28.6%. Mean annual discharge through the bridge was reduced 40%. Reduced overland sheet flow (from 80% of the time to 59% of the time), and lowered water levels would allow

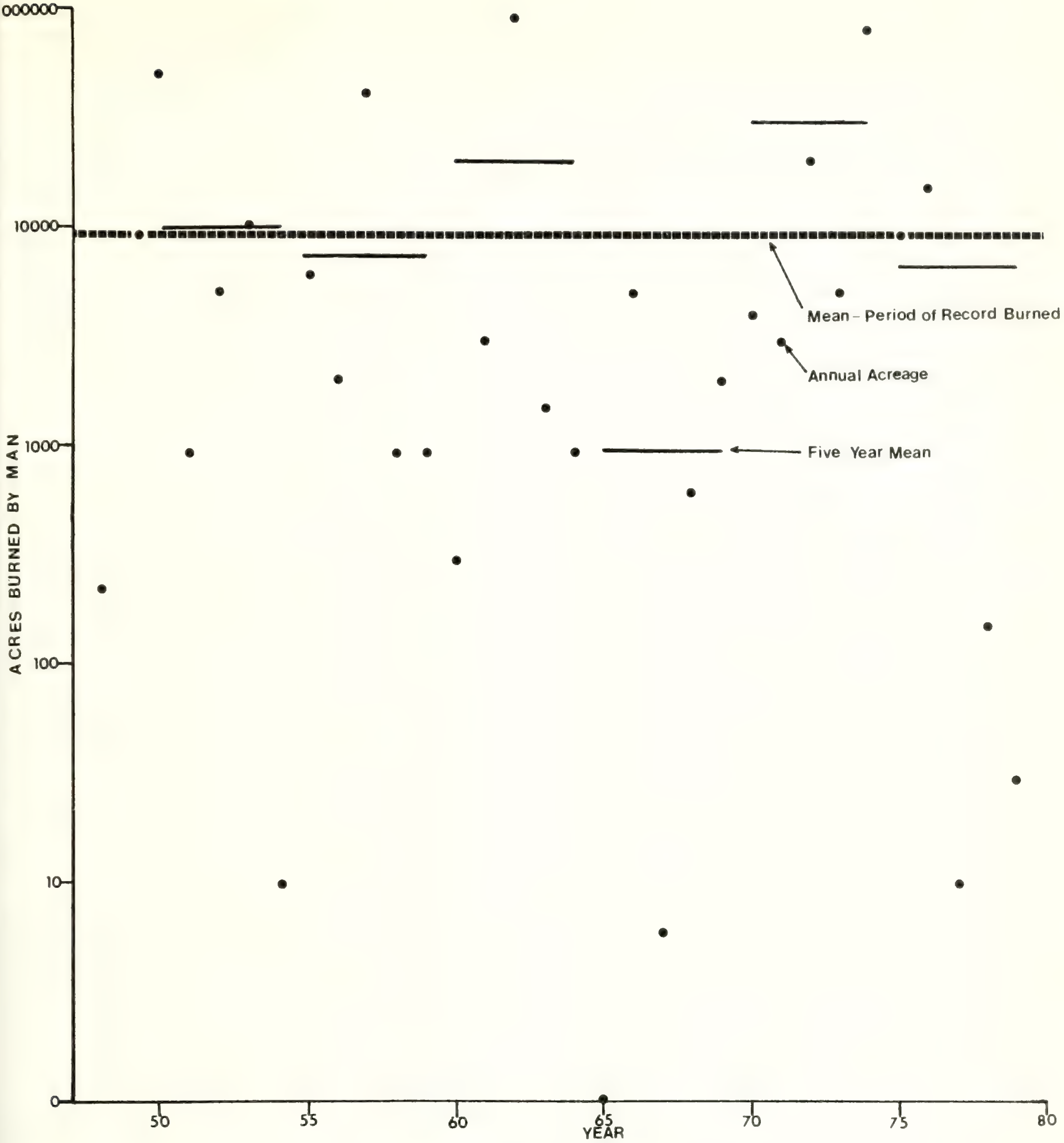

Figure 4. Semi-log graph of acres burned by man-caused fires.

more fires to burn more acres each month of the year.

Urbanization, which is continuing at an explosive rate (Wade et al. 1980), will require land and water, and will continue to change natural ecosystems. Keeping smoke from urban areas will be more and more difficult. Man-caused winter and spring dry season fires burn large areas, consume organic soil, and can contribute to the spread of exotics. These exotics are colonizing large areas at the expense of native vegetation, and crown fire is now possible for the first time in south Florida (Wade in press). According to Wade et al. (1980) the situation has become critical in south Florida, and the future will require decisions made upon realistic goals for resource protection.

Everglades National Park has an extensive prescribed fire program to control fuel, and a research program has been started which will document frequency and season for fire in the Big Cypress National Preserve. Prescribed fire is used on other state and federal lands (fig. 1). New legislation allows prescribed burning in hazardous accumulations of wildland fuel on private holdings, provided the owner does not object (Wade and Long 1979). Whether these activities will allow restoration of a natural fire regime in the face of extreme environmental perturbations remains to be seen.

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Fire History of a Western Larch/Douglas-Fir Forest Type in Northwestern Montana[1]

Kathleen M. Davis[2]

Abstract.--Mean frequencies were about 120 years for valleys and montane slopes and 150 years for subalpine slopes in this western larch/Douglas-fir forest from 1735 to 1976. Fires were small and moderately intense with occasional high intensity runs. Single burns thinned the overstory favoring mixed conifer regeneration. Multiple burns created homogeneous stands or shrubfields.

INTRODUCTION

In coniferous forests of North America fire is recognized as an ecological agent of change that, in some cases, is essential for continuation of certain biotic communities (Muir 1901, Intermountain Fire Research Council 1970, Kilgore 1973, Wright and Heinselman 1973). Acknowledging this as an integral factor of some environments, Mutch (1970) hypothesized that floral species in a fire-dependent community have flammable characteristics that promote fire. Features such as volatile oils, high resin content, serotinous cones, and fibrous bark perpetuate fire as a major ecological influence. However, in a community that is not fire dependent, species do not display flammable characteristics.

As an environmental factor, fire has direct and indirect effects on all resources; soil, water, air, animals, vegetation, etc. Provided with fire history information, land managers have an ecological basis on which to suppress fires, develop fire prescriptions, and evaluate planning alternatives in order to maintain and restore natural resources. Knowledge of the pattern, behavior, and effects of historic fires gives facts to develop logical resource programs.

PURPOSE

This study was undertaken to refine sampling techniques and extend fire history investigations in western Montana into a more mesic forest type and climate than encountered by Arno (1976) in the Bitterroot Valley of the Bitterroot National Forest.[3] Coram provided a contiguous study unit with documented history of logging operations and fires since the 1920's. A fire history investigation would be a continuation of research in this Bioshpere Reserve. Specific objectives of the study were:

1.--Field test the fire methodology that was being prepared by Arno and Sneck and develop techniques for sampling logged areas and mesic forest types.

2.--Determine and describe fire history through scar analysis and stand age class structure.

3.--Interpret the role of fire using the study results and historical information from surrounding areas.

GENERAL DESCRIPTION

Coram Experimental Forest was established by the US Forest Service on June 21, 1933, for the purpose of studying the ecology and silviculture of western larch (Larix occidentalis) forests. In recent years, research projects have included other forest resources and ecological influences such as watershed, soils, pathogens, insects, and fire. The forest is located on the Hungry Horse Ranger District of the Flathead National Forest in northwestern Montana about 11 km (7 mi) south of Glacier National Park and 34 km (21 mi) northeast of Kalispell, Montana.

Coram encompasses 2984 ha (7460 ft) of the western slopes of Desert Mountain drained by Abbott Creek. The landform was created by glacial activity. Elevations rise from 1006 m (3300 ft) on Abbott Flats to 1911 m (6370 ft) on the mountain top. Slopes vary up to 80%. Soils are loamy-skeletal, and much of the area has a thin layer of volcanic ash just below the soil surface.

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[1] Paper presented at the Fire History Workshop. (University of Arizona, Tucson, October 20-24, 1980).

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[3] Fire history of Coram Experimental Forest was studied as partial fulfillment of a Master of Science degree in 1977. The study was supported with a cooperative agreement between the Research, Development, and Application Project, Northern Forest Fire Laboratory, US Forest Service, and School of Forestry, University of Montana, Missoula.

Coram has a mean temperature of 16°C (61°F) in summer and -7°C (19°F) in winter, and annual precipitation is about 760 mm (30 in). Seasons are distinct. Snow may fall in early October and last until May in the high elevations. Summers are short and cool with the most favorable fire weather occurring during the driest months, July and August. Summer thunderstorms approach in the late afternoon from the southwest and are usually weakened by the time they reach the forest since they have travelled over several mountain ranges. It has been noted that fewer lightning fires occur in forests of northern Idaho and MOntana than in forests to the south (Barrows 1951).

This is a western larch/Douglas-fir forest type (SAF 212). Habitat types according to Pfister et al. (1977) are *Abies lasiocarpa*/*Clintonia uniflora* h.t. (subalpine fir/queen cup beadlily); *Abies lasiocarpa*/*Menziesia ferruginea* h.t. (subalpine fir/menziesia); *Abies lasiocarpa*/*Linnaea borealis* h.t. (subalpine fir/twinflower); *Abies lasiocarpa*/*Xerophyllum tenax* h.t. (subalpine fir/beargrass); *Pseudotsuga menziesii*/*Physocarpus malvaceus* h.t. (Douglas-fir/ninebark); *Tsuga heterophylla*/*Clintonia uniflora* h.t. (western hemlock/queen cup beadlily); and *Abies lasiocarpa*/*Oplopanax horridum* h.t. (subalpine fir/devil's club).

The forest canopy becomes open at high elevations and there are very few trees on the top of Desert Mountain. Here where local climate is cold, soils are poorly developed, and snow lingers, vegetation cover is hardy perennial herbs. On lower slopes the forest is dense and continuous. Mixed conifer stands are common but small pockets of larch, lodgepole pine (*Pinus contorta*), Douglas-fir, subalpine fir, and hemlock do occur. Spruce (*Picea glauca* x *Picea engelmannii*) is found in mixed stands mainly with Douglas-fir and subalpine fir. Ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*), and whitebark pine (*Pinus albicaulis*) are scarce.

Light to medium fuel loadings prevail throughout. Undergrowth, litter, and debris less than 8 cm (3 in) diameter constitite the bulk of the ground fuels. Heavy accumulations occur as downfall where intense fires have burned or Douglas-fir bark beetle have occurred. Fuel model H is appropriate and depicts a situation where fires are typically slow spreading becoming intense only in scattered areas where the downed woody material is concentrated (Deeming et al. 1978).

METHODS

The methodology used to investigate fire history in forested and logged areas is described by Arno and Sneck (1977). The techniques were a simple process of aging and correlating dates of scars and identifying age classes of fire-initiated regeneration.

Transects were laid out in a network to cover all elevations and aspects. They were subjectively placed to maximize sampling obvious burns and other areas likely to have scarred trees and regeneration, such as ridges. Trees that were sampled were locate on or adjacent to the route. When a transect crosse a logged unit, the area was intensively and systematically examined in a zigzag pattern that covered the cut.

The method suggested by Arno and Sneck is a reconnaissance walk of the network to identify and locate the best scarred trees then a second walk to collect samples. However, since trees with external scars were scarce and since most trees had only one scar, the plan was changed to sample from scarred trees and stumps on the first walk.

Sampling procedures entailed:

1.--Describing habitat types and existing vegetation.

2.--Cutting cross sections with a chainsaw from scarred trees and stumps (or making field counts on stumps when unable to get a sound cut).

3.--Coring fire-initiated regeneration to age stands.

4.--Describing in detail all trees, stumps, and regeneration sampled.

Adjacent logged areas of the Flathead National Forest were selectively studied when it became obvio that Coram's history was different from the extensiv stand-replacing fires reported for surrounding fores The purpose of examining outlying areas was to look for evidence of past fires in order to better understand the history of the region and draw a compariso for Coram.

Attempts were made to document each fire year with a combination of cross sections, stump ring counts, or stand age classes. For some years this was not possible because of limited evidence. Cross sections were cut from lower tree trunks at a positi to obtain the best scar and pith record. Annual rin on unsound stumps were counted enough times to obtai a good estimate of fire scar and pith dates. Cores to age regeneration were mainly taken from seral trees, usually larch, lodgepole, and Douglas-fir. In a few cases the climax species were used to age stands when it was obvious they represented the immediate post fire sere. All sampling was done at approximately 0.3 m (1 ft) height to obtain more accurate dates and standardize the information.

Total age for each sample was determined by adding to the pith count the estimated number of years for each species to reach 0.3 m. Throughout the study area, several seedlings of all species about 0.3 m tall were aged. This resulted in a grow factor by species for the period between germination and attaining 0.3m in height. Factor for larch, lodgepole, ponderosa, and white pine was four years, for Douglas-fir five years, and subalpine fir, whitebark pine, and spruce was six years. A ten year span was allowed as the maximum time for establishment after fire because of the many factors influencing seed germination and development.

In the laboratory, cross sections and increment cores were air dried, sanded or shaved, and examined with a binocular microscope. Ring counting proceeded from the cambium to the pith and was taken on at least three separate occasions to verify the dates. When the pith was not included, the number of additional rings to the pith was estimated by projecting the curvature and thickness of the innermost rings.

To aid analysis of fire frequencies, tree and stump data were arranged into stands based on habitat type, geographic locale, species, fire chronology, and regeneration information. Fire history was determined from individual chronologies of each stand member. The largest amount of evidence for a certain date, particularly from samples with clear ring formations, indicated the probable fire year. Dates were synchronized by moving scattered dates ahead in time (false rings) or back (missing rings) towards the fire year. Minor ring errors do not allow for precise detection of fire years so it was hypothesized that two separate scarring intensity fires did not occur within three to four years of each other in one stand. This span was selected since the scattering of dates around a year was usually within this range. Chronologies for all stands were compiled to develop a master chronology.

RESULTS AND DISCUSSION

Techniques to sample logged units and an area of infrequent fires were added to the methodology developed by Arno in a drier forest type. The successful application of the basic methodology with slight variations indicated it is generally applicable to inland coniferous forests of western North America in locations where ring counts furnish reliable data.

Vast areas of seral forest communities, mosaic vegetation patterns, fire-scarred trees, and charcoal verify the prevalence and ecological importance of fire in forests of the northern Rocky Mountains. Coram Experimental Forest is no exception. Historical evidence showed that fire has been a regular and widely occurring ecological factor.

A total of 136 scars were examined on 130 trees and stumps. Only one-fifth of the data was obtained from live trees because open scars (catfaces) were uncommon. They were generally found on thin-barked lodgepole pine, subalpine fir, spruce, and whitebark pine. Fire resistant, thick-barked western larch and Douglas-fir usually had healed scars (buried). These were undetectable on the trunk but readily could be identified on cut stumps. Consequently, information found in logged areas was essential to determining fire occurrence.

Thirty-five fire years were documented from 1602 to 1976. Fire years from 1602 to 1718 should be considered as approximate because sample sizes were small and accuracy diminishes with time. From 1718 to 1976 they are probably within a year of the actual date because more evidence was available. When dates are based solely on stand age classes they were felt to be within three to five years of the actual date. It is difficult to pinpoint fire years by age classes because of factors which can delay seedling establishment and development.

The master fire chronology undoubtly does not include all fires occurring during the record period since some small area burns would have been missed by the transect network. Moreover, it is extremely difficult if not impossible to record low intensity fires which do not leave long-termed evidence, such as scars, regeneration, or vegetation moasics. This was confirmed by the difficulity of relocating suppressed lightning fires that had been mapped.

The term "fire frequency" as used here denotes the number of years between fires or the fire-free interval. To calculate frequency, logical time periods were established. Prior to 1735 the chronological information became too sparse and frequency could not be accurately determined. From 1735 to 1910 was designated the "historical fire" period when lightning was the principal cause. The period from 1911 to 1976 was the "fire suppression" period when concerted efforts were made to contain fires since extensive control forces were organized after the notorious fires of 1910.

Average frequency was calculated for the historical fire period (1735-1910) in order to determine the occurrence of lightning fires. This was done for topographic units by computing frequency for each stand then obtaining the average of the stands in each habitat type (table 1). Thus, mean fire-free interval represents the average reoccurrence of fire on a particular site. Since fire may kill trees in a stand or, conversely, leave little evidence, frequency is referred to the site. Minimum and maximum fire-free intervals are the range of actual frequencies.

Mean fire-free intervals displayed in the table may seem long, but most stands had just one fire recorded for the historical fire period. The exceptions were three stands that had up to six fires. Long intervals are also substantiated by the fact that most trees had only one scar, because once a tree is scarred it is more susceptible to injury due to exposed, dry wood and resin accumulations around the wound. Although differences were not large, there was a trend of decreasing mean frequency with increasing elevation. On north aspects, fires were least frequent and most intense. As would be expected, multiple burns occurred primarily on south facing slopes.

Between 1602 and 1976, fire occurred somewhere in Coram on an average of every 11 years, and for the historical period it was every 12 years. During the suppression years (1910 to 1976) frequency averaged 7 years, but most burns occurred between 1910 and 1930. This may be due in part to extended

Table 1.-- Fire frequency between 1735 and 1910 by habitat type for Coram Experimental Forest, Flathead National Forest. Frequencies are based on all fire years identified within stands.

Topographic description	Habitat type[1] groups	General elevation range (meters)	Dominant trees with continued fire exclusion (most abundant species first)	Dominant trees before 1910 (most abundant species first)	No. of stands (no. of trees)	Mean fire-free interval (min-max interval[2]
Valleys	ABLA/CLUN h.t., ARNU phase ABLA/CLUN h.t., VACA phase	1000-1140	Douglas-fir western larch	western larch Douglas-fir	2 (15)	>117 years[3] (21-175)
Montane slopes	PSME/PHMA h.t., CARU phase PSME/PHMA h.t., PHMA phase ABLA/CLUN h.t., ARNU phase ABLA/CLUN h.t., VACA phase ABLA/CLUN h.t., XETE phase ABLA/CLUN h.t., PHMA phase[4] ABLA/CLUN h.t., CLUN phase ABLA/LIBO h.t., VACA phase	1200-1650	Douglas-fir western larch	Douglas-fir western larch lodgepole pine	11 (88)	121 years (6-173)
Lower subalpine slopes	ABLA/CLUN h.t., XETE phase ABLA/XETE h.t.	1575-1800	subalpine fir Douglas-fir	subalpine fir Douglas-fir lodgepole pine	3 (15)	146 years (47-132)
Upper subalpine slopes	ABLA/XETE h.t.	1800-1910	subalpine fir Douglas-fir	subalpine fir lodgepole pine whitebark pine	3 (8)	>146 years (47-175)

[1] Habitat types according to Pfister et al. 1977.

[2] The maximum interval was the longest fire-free interval within the period 1735 to 1910. For example, 175 means no fire between 1735 and 1910. The minimum interval was the shortest interval between fires during the period. The mean interval is the average frequency.

[3] The "greater than" sign denotes some stands had no fires between 1735 and 1910, so frequency was stated as 175 years for computation.

[4] ABLA/CLUN h.t., PHMA phase was a locally occurring variation of ABLA/CLUN h.t. only found in a small area of Coram Experimental Forest dentified by Pfister (1976 personal communication).

drought conditions between 1916 and 1940 (Wellner 1970) and increased settlement. It is interesting to note that 20 lightning fires have been suppressed since 1920. Thirteen of these were extinguished between 1920 and 1940.

Fires were small and usually stopped along ridges, ravines, and creeks which suggested that fuel availability and local weather influences controlled spread and intensity. Cloudy, rainy days that typically follow thunderstorms would contribute to moderate behavior. The three largest fires that occurred in 1832, 1854, and 1892 each covered only 100 to 190 ha (250 to 475 ac). No evidence of extensive, stand-replacing fires anywhere indicated that such fires are not typical of Coram. Fragments of charcoal in the soil, however, showed that past fires occurred widely throughout the forest.

Low to moderate intensity fires were common on montane slopes, but intensity increased at ridgetops or on steep slopes with heavy fuels. Fire functioned primarily as an agent of change that thinned stands, reduced fuels, rejuvenated undergrowth, and prepared seedbeds. Seral species, particularly western larch, Douglas-fir, and lodgepole pine, were promoted. In the high elevations, lodgepole pine and subalpine fir were the post fire sere under their own canopies. In the absence of fire, shade tolerant species became dominant.

The effects on vegetation varied with fire frequency, behavior, and intensity. Infrequent, moderately intense burns were most prevalent. They resulted in regeneration of mixed conifer stands commonly with small pockets dominated by a seral species. Severe burning created a more definite even-aged structure. Intense, multiple burns within a short time (<50 years) reduced the original stand and modified the species composition, generally favoring lodgepole pine or shrubfields.

Most of the perennial undergrowth species are capable of sprouting as long as the regenerative tissue is not killed by high temperatures. Moderately intense fires rejuvenated plants by burning decadent parts and stimulating new growth. Multiple and intense fires that reduced the overstory and halted succession also created conditions which favored shrubs and grasses. Herbaceous plants preferring shaded, cool microclimates decreased in abundance at least immediately after fire.

In logged units around Hungry Horse Reservoir, 24 stumps provided information for 18 fire years. Sampling confirmed fire years, areal spread, and multiple burns that were mapped by the Forest Service. It also gave evidence of older and less obvious burns. Frequency was slightly greater than for Coram, which is in accordance with other fire history studies.

Other investigators documented the character and effects of past fires in the region (Ayres 1900a

1900b, Gabriel 1976, Antos 1977). All emphasized the severe, extensive fires and cited changes in vegetation composition, especially replacement by dense stands of lodgepole pine. Shrubfields created by multiple burns were also common. Furthermore, each mentioned the occurrence of low to moderate burns that thinned stands, primarily changing the structure more than composition. These burns typically occurred in small drainages on the side of larger valleys or in mesic valley bottoms.

In 1929 the intense Half Moon Fire almost entered Coram when it burned just to the south on Lion Hill and the present-day site of Hungry Horse Dam. A few days after the headfire went up the drainage of the Flathead River, the eastern flank became active and burned towards Coram resulting in an explosive fire on the steep north facing slopes of Belton Point on Desert Mountain (Gisborne 1931). Strong, cold drafts pulled in by the convection of the blow up subdued the flames along the ridges running south and west from the point. If winds had not stopped the flaming front, the fire would have burned into Coram.

In summary, information obtained from the experimental forest was compiled with data from the extended study area, literature, and records to gain an understanding of fire regimes for and around Coram. Coram's fire history is not representative of most of the surrounding forested lands that experienced extensive, stand-replacing fires. However, it is not atypical of the region. Several accounts and vegetative evidence of moderately intense fires proved these are widespread occurrences, especially in moist valley bottoms, topographically isolated drainages, and high elevations. Coram is a small, mesic valley that has little lightning activity except on top of Desert Mountain. The valley is topographically isolated, being protected by high ridges of Desert MOuntain. Low to moderate fires are the history of Coram, but judging from the surrounding areas, it is conceiveable that intense fires could occur in the future.

MANAGEMENT IMPLICATIONS

In this western larch/Douglas-fir forest type, fire is the primary ecological agent of disturbance that creates mosaics of vegetation composition and structure and, in turn, affects interrelated biotic and abiotic components. Mean frequencies range from 120 to 150 years within different topographic locations in an area where suppression has been carried out for roughly 50 years. The effect control has had depends when exclusion started in the fire cycle. The fact that 20 lightning fires have been suppressed since 1920 is reason to believe changes that would has occurred were prevented.

The management implications are straightforward. An important ecological factor is being successfuly excluded, at least until now. If variety and stability of heterogeneous forest communities are desired, then fire ought to be restored. This can be done by incorporating prescribed burning into existing programs for wildlife, silviculture, natural fuel reduction, insects, diseases, watershed, etc. It can also be accomplished by establishing fire management zones wherein fire (natural, prescribed, or accidental) is allowed to burn during predetermined conditions.

When suppression is necessay, managers would do well to examine areal spread, regeneration, frequency, and other signs of past fire behavior to tailor control tactics when possible. In a location like Coram, the best method may be indirect attack to catch fires at topographic or vegetative breaks where most historically stopped. In areas where large, extensive fires are obvious, it would be wise to have strong control forces available or to get out of the way of the headfire. By using knowledge gained from past fires, managers can evaluate effective suppression methods beforehand and be aware of safety hazards for firefighters.

Fire history studies are planning tools. They are essential information for developing logical fire management plans. Even if the plan is total suppression it is important to know potential fire behavior and fuel situations as well as ecological consequences of fire exclusion. In addition, historical studies provide pertinent data for a variety of planning; such as wildlife management, watershed management, forest-wide planning, resources management, recreation planning, and forest pest control. Where fire is an integral factor, it must be acknowledged and incorporated into planning efforts.

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Fire History — Blue Mountains, Oregon[1]

Frederick C. Hall[2]

Interpretation of underburning effects in mixed conifer/pinegrass plant communities (Blue Mountains, Oregon) suggest: underburns occurred at 10-year intervals; ponderosa pine is being replaced by white fir; pine stands did not develop according to "normal stand development"; pine stands require stocking level control to prevent stagnation; range condition must be rated on successional vegetation not climax; range grasses show "downward range trend" due to increasing tree cover complicating trend interpretation; herbaceous plants can sustain livestock use since they developed genetically under periodic 100 percent use by fire; livestock fill a major biotic niche not occupied by wildlife; some plants are dependent upon fire for regeneration; some wildlife depend upon stocking level control and successional trees (pine and larch) formerly provided by underburning; soils developed under fire and are brown forest rather than podzolic; fire hazard is changing from light, flashy fuel under open tree cover to heavy fuels under dense tree cover.

INTRODUCTION

Fire in Western forests has been common. Its fluence on vegetation and soil was studied in njunction with a comprehensive ecological evaation of the five-million-acre (two-million-ctare) Blue Mountain land mass in Eastern Oregon d Southeastern Washington. Both conflagration re and natural underburning have left their mark. ant communities dominated by lodgepole pine or stern larch are the result of conflagration fire. contrast, underburning effect on vegetation is ten difficult to see. In this paper I will deal ly with underburning. Evidence will be presented document underburning frequency, the influence re had on tree dominance, interaction effect tween tree cover and ground vegetation, fire fluence on genetic development of ground vegetaon, influence underburning had on soil developnt, and implications these have for land nagement.

I will illustrate interactions of fire with egetation in the ponderosa pine/pinegrass cosystem one of 18 kinds of forest communities the Blue Mountains (Hall 1973). We name plant communities by the dominant tree, shrub, and herbaceous species. In this case, shrubs are absent; therefore, we call it the ponderosa pine/pinegrass community. It occupies nearly one-fifth of the total acreage in the Blue Mountains.

EVIDENCE OF UNDERBURNING

Underburning has been common in the Blue Mountains as shown by numerous fire-scarred trees. A fire scar is a storybook, a history of fire. The easiest way to open the storybook is shown in Figure 1. When cut in cross-section, a number of ripples or waves can be seen. Each one of these waves indicates the occurrence of a fire.

The waves or ripples are formed as follows (Fig. 1). While the tree is young, lightning strikes the ground and starts a fire in the easy-to-ignite pinegrass. Fire burns over the ground to the base of the tree igniting an accumulation of pine needles. A hot fire will scorch part of the bark on the tree, resulting in death of the cambium. Eventually, the dead bark will fall away as the wound begins to heal. When this happens, the tree will usually produce pitch at the point where new bark begins to grow around the wound. Some years later lightning strikes again, burns through grass, into needles at the base of the tree, and ignites the pitch. The pitch burns up the side of the tree, killing bark at the edge of the wound. This bark falls away as the tree again grows around the wound. Later, lightning strikes again, burns through the grass and ignites the pitch, killing the bark.

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[1] Paper presented at the Fire History rkshop, University of Arizona, Tucson, Arizona, ctober 20-24, 1980.

[2] Frederick C. Hall is Regional Ecologist, acific Northwest Region, U.S. Forest Service, rtland, Oregon.

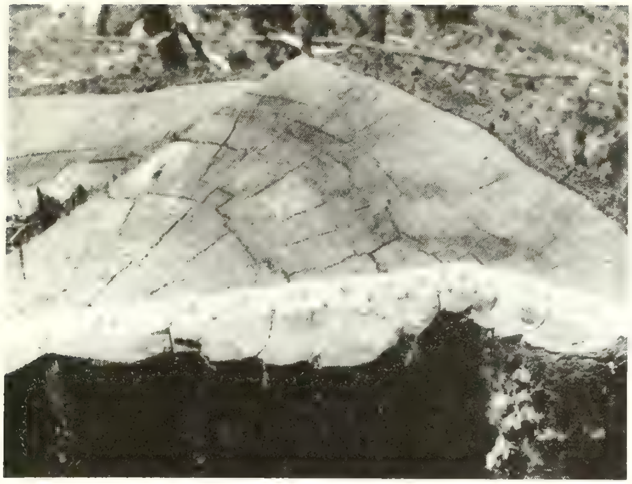

Figure 1. Cross-section of a fire scar. Tick mark at left indicates the tree center and the year 1763. Numbers between tick marks indicate years between marks. Each tick mark locates the annual ring of the year in which fire damaged the tree.

In Figure 1, the date was 1763 when this ponderosa pine reached 18 inches tall (stump height). From then, the tree grew for 26 years before underburning damaged the bark and cambium, forming a first fire scar. Each number on the tape between the tick marks indicates the number of annual rings between fire scars. After the first scar, the tree was damaged at yearly intervals of: 9, 10, 13, 8, 10, 10, 5, 9 , 6, 15, 9, 38, and 36 years. The fire scar occurring between 6 and 38 was 1893. Ten years later, the United States Forest Service began fire prevention in this area. Therefore, the next fire did not occur for 38 years. Since then, the tree grew for 36 years until it was cut in 1967.

This stump shows a fire scar being produced about once every 10 years prior to the start of protection of forest lands from wildfire in 1904. The 10-year average is a maximum time between underburnings. Lightning could have ignited pinegrass and burned up to the tree without causing a fire scar if pitch or needles were not present. We have evidence here that fire burned at least once every 10 years. I feel that underburning has been a normal part of the environment in the Blue Mountains (Hanson 1942). In 1973, 220 fires were started by lightning in the Blue Mountains; an average of one fire for each 23,000 acres each year (Anon 1973).

FORESTRY

Recurrent underburning in the ponderosa pine conifer/pinegrass plant community maintained a very open stocking of trees by periodic thinning. Groups of young ponderosa pine under significant Competition could not grow fast enough in diameter or height to escape the fires. This means that ponderosa pine stands did not develop according to the classical concept of "normal stand development" (Meyer 1961). Normal stand development suggests that thousands of seedlings become established, some seedlings grow faster than others, become dominant, suppress their neighbors, and finally eliminate the suppressed trees from the stand. With fire control, hundreds and sometimes thousands of young ponderosa have become established per acre.

These young trees have not grown according to normal stand development theory; instead they have almost universally become stagnated. We have found little evidence in the Blue Mountains to indicate that ponderosa pine can, within a 50- to 100-year timespan, break out of stagnation. Instead trees persist and grow in diameter at 50 to 70 rings per inch and in height at 4 to 6 inches per year to at least age 80. Douglas-fir, white fir, lodgepole pine and western larch behave similarly.

Height and diameter growth of trees which developed with recurrent underburning is entirely differ en. Increment cores show diameter growth (BH) of three to five rings per inch at the center of a tree. Rate of diameter growth gradually slowed as stand density increased. This suggests that initia stocking density of most nautral pine stands was quite low. Low stocking density is further supported by presence of large dead limbs close to the ground. Many old-growth ponderosa pine still retai limbs two to four inches in diameter in the lower third of the bole which could only develop under open stocking.

The relationship between underburning and tree stocking has important land management implications. First, stocking level control is mandatory. Overly dense young stands must be pre-commercially thinned so tees can grow to commercial size. Once of commercial size, periodic thinning is desirable to prevent stand stagnation and reduced growth. A second concern deals with estimating allowable cut volumes. Some methods accept "fully stocked stands" as contributing a full share to harvestable volume. Small-diameter stagnated stands of pre-commercial size will not furnish future scheduled harvestable volume.

The typical stand is forty years old, eight feet tall, two inches DBH and growing at 50 rings per inch (0.4 inches diameter growth in 10 years). A land manager dealing with ponderosa pine, Douglas-fir or white fir in the Blue Mountains is not fat and happy with "well-stocked stands." Instead, he has an economic liability on his hands requiring stand treatment prior to realizing an economically saleable product. The manager should be more satisfied with "understocked stands" which will grov rapidly to a suitable diameter.

Underburning has affected trees in another way. Fire has selectively killed white fir and Douglas-fir while favoring ponderosa pine due to highly different bark conditions. Pine develops fire-resistant bark containing a one-eighth-to one-fourth-inch-thick dead outer layer at about two inches diameter. Fir bark remains green and photosynthetically alive up to four inches diameter. This bark is so sensitiv to heat that fire burning quickly through pinegrass is able to kill the bark and destroy the tree. In fact, white fir bark is so sensitive to heat that understory trees released by overstory removal ofter suffer sunscald due to temperatures created by direct sunlight. With the demonstrated success of wildfire suppression, ponderosa pine is being replaced by white and Douglas-fir. By eliminating underburning, we have changed the environment to such an extent that a new "primary" succession is taking place. The ponderosa pine/pinegrass community is changing to a fir/pinegrass-heartleaf arnica plant community "mixed conifer/pinegrass" rather than ponderosa pine/pinegrass. Our data indicates that cubic volume productivity of wood is about 20 percent greater when the site is dominated by firs than when it is dominated by ponderosa pine. (Hall 1973).

Realizing that underburning has tended to favor ponderosa and discourage white fir is significant information for the land manager. He has the opportunity of growing at least three different tree species on this site instead of just ponderosa. He has an opportunity of increased fiber production by converting pine to fir. But he should note that fir only regenerates under a shelterwood often of ponderosa pine, whereas ponderosa can regenerate in full sunlight. This means silviculture for maintaining ponderosa pine is different from Douglas-fir or white fir.

Lack of underburning has apparently retarded growth of ponderosa pine trees. On several sites we compared height and diameter growth between ponderosa pine and white or Douglas-fir in full sunlight under low stocking conditions. On one site, ponderosa was 41 years old, 2 inches diameter, and 8 feet tall. Within 10 feet of this tree in equally full sunlight was a white fir 20 years old, 3 inches diameter, and 18 feet tall. Pine grew 6 inches in height last year and the fir grew 20 inches in height; Pine averaged 40 rings per inch diameter growth and fir averaged 13 rings per inch. Old-growth ponderosa on this site, which developed with periodic underburning, showed 3 to 5 rings per inch diameter growth at the tree center and 5 to 7 rings per inch at 3 inches DBH. Something seems to inhibit growth of ponderosa pine while not adversely affecting white fir or Douglas-fir.

I suspect a selective inhibitory substance in ponderosa pine litter that is destroyed with periodic underburning. Without fire, this substance is free to build up in the soil and reduce pine growth. Measurements on underburned stands have suggested increased diameter growth of pine compared to unburned controlled plots. A somewhat analogous situation has been found in France with Norway spruce. Under dry summers and buildup of tree litter, manganese reaches concentrations that prevent regeneration of spruce. It does not prevent regeneration of beech and maple. Consequently, the land manager in France must grow alternate rotations of spruce and hardwoods or destroy the toxic manganese in litter by scarification (Duchaufour and Rousseau 1959). In this country, pine litter has been shown to influence root growth of various grasses and forbs (Jameson 1968, McConnell and Smith 1971).

RANGE

Underburning has had both a direct and indirect effect on ground vegetation; directly by burning and indirectly by permitting tree cover to increase. Fire-dependent ponderosa pine/pinegrass produces 500 to 600 pounds of forage per acre in pinegrass and elk sedge under 50 percent tree crown cover. As pine is replaced by fir, tree crown cover increases significantly. This crown cover drastically reduces ground vegetation under 100 percent tree cover, grass production is only 50 to 100 pounds per acre and heartleaf arnica becomes apparent. Clearly, control of underburning has not only caused an increase in fir and a change in tree dominance but also has caused a dramatic shift in ground vegetation.

This shift in ground vegetation has significant livestock management impacts. In 1940, 64,000 animal units grazed in the Blue Mountains for three months. By, 1970, 10,000 animal units were lost because of increasing fir cover, a 16 percent reduction. An animal unit is one cow and her calf or five to seven sheep. This reduction represents not only a significant financial impact on ranchers dependent upon National Forest land but it also significantly reduces red meat for the consumer. In 1940, the Blue Mountains supplied 64,000 people with their one-year supply of beef (114 pounds per person per year). By 1970, only 54,000 people were supplied. Even though population of the United States increased, the ability to produce red meat was eliminated for 10,000 people.

Changing ground vegetation due to tree cover poses a problem in evaluating condition of the rangeland and trend in dominance of forage plants (Dyksterhuis 1949, Ellison 1951). In "typical" rangeland evaluation, good condition is equated with climax vegetation dominance. If livestock are forced to overgraze the range, they kill the most palatable forage plants, causing a downward trend in their dominance. The range is then considered to be in fair or poor condition. This very same situation is occurring without livestock influence in the mixed conifer/pinegrass community. Pinegrass and elk sedge, the most palatable plants, decrease with increasing tree cover. Interpretation of range trend must separate changes in ground vegetation caused by tree cover from those caused by livestock impacts. Interpretation of trend is our best means of appraising current livestock management--we strive for no downward trend in good range condition or upward trend in fair or poor condition.

On forest areas, condition of the rangeland must be related to tree cover instead of climax ground vegetation dominance. The climax condition under 100 percent fir cover is not a suitable benchmark for estimating how much pinegrass and elk sedge should occur under a 50 percent crown cover of pine. Range condition guides must relate tree cover to composition, density and productivity of ground vegetation.

Big-game animals, deer and Rocky Mountain elk, suffer the same reduction in forage as livestock. In addition, variety of palatable plants is significantly reduced. In the ponderosa pine/pinegrass fire community, five to eight plants contribute significantly to deer and elk forage. In the dense fir/pinegrass-arnica community, only three plants significantly contribute forage.

Underburning has had a direct effect on ground vegetation. Fire had to be carried by ground vegetation. Thus, pinegrass, elk sedge, balsam woollyweed, vetch, arnica, strawberry, and all other ground vegetation plants in this community developed genetically under 100 percent utilization every few years. Those plants best able to compete and colonize the site became dominant. Nature selected these plants genetically in the same way we breed and select pasture or hay grasses. Various species and varieties are mowed at two- or three-inch stubble heights to evaluate their performance under use. Those which perform best are selected to produce pasture or hay. Periodic burning has endowed pinegrass and elk sedge with the ability to withstand utilization by livestock. They can persist and increase under natural range conditions with 25 to 40 percent utilization every single year.

Some plants often found in this plant community, like the shrub ceanothus, need fire for continued survival. Ceanothus seeds require heat treatment by underburn or conflagration fire to trigger germination (Hickey and Leege 1970). With fire suppression, many stands of ceanothus have not regenerated. This shrub is desirable because it provides cover and essential early spring, late fall and winter forage for game animals, and it adds nitrogen to the soil. The current means of maintaining ceanothus is logging and use of fire for residue reduction.

Use of prescribed fire in mixed conifer/pinegrass has produced other results. In no case has a species been eliminated by burning; instead from one to three new species appear, particularly legumes such as lupine and vetch. In all cases, herbage production has increased the year following burning ranging from 20 to 35 percent and persisting for another 1 to 3 years. And palatability of pinegrass is increased when fire is hot enough to burn at least half the duff layer. Cool fire, burning the leaf litter and no duff, does not effectively stimulate legumes, herbage production or palatability.

ECOLOGY

Effects of underburning on both trees and ground vegetation has raised some interesting ecological questions. For example, what is climax: pristine, fire maintained ponderosa pine/pinegrass or the newly developing white fir/pinegrass-arnica kind of plant community? Classification and study of plant communities often uses climax as a point of reference (Daubenmire and Daubenmire 1968, Odum 1971, Oosting 1958). But how can "climax" without fire be estimated if most stands have never been in climax? Fire suppression was initiated about eighty years ago which hardly seems long enough for a climax to have developed.

Another implication of climax is that greatest species diversity occurs in this condition (Odum 1971). Vegetational succession in the mixed conifer/pinegrass type clearly suggests decreasing species diversity as climax status is approached. For example under pine canopies of 50 percent, 15 ground vegetation species constantly occur and three tree species can regularly be found. Under climax conditions, white fir clearly dominates to the exclusion of ponderosa pine and generally Douglas-fir, and only 7 ground vegetation species constantly occur, none of which are legumes or shrubs. As a result, wildlife diversity is also reduced. As noted earlier, 5 to 8 species are palatable to deer and elk under open pine while only 3 contribute under dense fir.

Climax has also been described as a "stable state" (Daubenmire and Daubenmire 1968, Odum 1971, Oosting 1958). This concept suggests that, barring some natural disturbance, the plant community is stable. The tussock moth epidemic, which occurred in the Blue Mountains in the early 1970's, indicates that climax is most unstable (Brooks, et.al. 1978). Total stand death only occurred where white fir was the sole tree species -- climax. Total stand death never occurred with a mixture of species -- successional pine-fir/pinegrass. A similar climax vs. successional relationship is occurring today with a western pine beetle epidemic. Apparently climax is a condition where plant succession is very slow but is it also a condition highly susceptable to disturbance. An interesting combination of successional "stable state" with a disturbance "unstable state".

WILDLIFE

Underburning has affected wildlife in several ways: stocking level control of trees, encouragement of successional vegetation and high forage production. Previous discussions have pointed out the decrease in both herbage production and plant species diversity as mixed conifer/pinegrass changes form open pine to dense fir. This change decreases forage for wildlife and also changes wildlife habitat. Under fire, recently burned areas were foraging spots due to legumes and the stimulation of palatability, tall trees produced thermal cover, and occasional patches of regeneration afforded hiding cover (Thomas 1979). Climax stands seem to have uneven-aged structure which provides cover but little forage.

Past fire has been particularly important to the pileated woodpecker. This 14-inch-long bird prefers a ponderosa pine or western larch tree about 24 inches in diameter where it excavates its nest hole, usually over 40 feet above the ground which requires a tree about 30 inches DBH. Large, tall, successional trees suitable for pileated use were produced by underburning which encouraged pine and larch and also maintained stocking level control necessary for growing large diameters. But these circumstances were not optimum because underburning that produced large trees also burned up snags housing carpenter ants used as a staple winter forage supply. And the burning also tended to prevent an understory of trees characteristic of most-used pileated woodpecker nesting habitat. Optimum habitat is large, overstory pine or larch with an understory of trees less than 50 feet tall and a suitable supply of heart-rotted snags housing carpenter ants (Thomas 1979). This condition is presently common due to 80 years of fire suppression and seems to represent a mid-successional optimum for pileated woodpeckers. Climax without pine or larch is sub-optiomal as is fire maintained ponderosa pine/pinegrass.

Livestock grazing has suggested another specter of traditional thought. Wildlife are considered to have developed concurrently with vegetation and climate. In so doing, they have generally filled most habitat niches by one or more species (Moen 1973). Livestock currently fill a niche apparently unoccupied prior to white settlement. Historical reports of elk and deer suggest current populations are greater than under pristine conditions. In addition, livestock produce as much red meat today as all the deer and elk harvested in the Blue Mountains. At 6.1 million pounds, one might consider this a significant niche.

SOIL

We have seen that underburning was common in mixed conifer/pinegrass. By deduction, it would seem that soils have developed under periodic underburns in this plant community. For years, these soils caused consternation to soil scientists trying to classify them by European or eastern United States nomenclature. The mixed conifer/pinegrass plant community occurs in a northern type of environment characterized by snow cover during the winter (Montane Forest Formation) (Lutz and Chandler 1946, Oosting 1958). In Europe and the eastern United States, montane forests invariably grew on a podzol or podzolic soil. A podzol has a very dark A-1 horizon one to three inches thick, a white A-2 horizon three to six inches thick, and below that a B horizon of brown to dark brown. Mixed conifer/pinegrass soils do not show this sequence. Instead they gradually grade from dark to light brown. These have been referred to by Canadians as gray wooded or brown forest soils (Spilsbury 1963). They occur in the West under forest/grass plant communities that have been periodically underburned. Underburns consumed litter contributing to podzol development. Abundant grass roots have carried a brown to moderately dark brown color well down into the soil profile. Brown forest soils developed under periodic burning and are capable of withstanding periodic burning. In fact, if our supposition is correct that ponderosa pine litter inhibits ponderosa pine growth, it would seem desirable to consider periodic burning.

FIRE HAZARD

Fire hazard is directly correlated with changes in tree cover and ground vegetation. In open pine/pinegrass, about two tons of needle litter can develop in ten years between fires while herbaceous flashy fuel is only about a third of a ton. Heat from burning two tons per acre is easily dissipated through the open crown cover of pine. With a change from pine to fir, pine trees die and fall to the ground greatly increasing fuel and crown cover closes.

A near climax stand appears to have both overstory and understory fir with crown closure exceeding 100 percent. Cover greater than 100 percent is possible when cover of overstory and understory are measured separately. Up to 30 tons of moderate to heavy fuel cover the ground. When lightning strikes in this stand, the fire does not move quickly through light, flashy fuel but tends to burn hotter and slower in tree needles, twigs and old trees. This heavier fuel produces more heat and the closed crown canopy does not permit heat to escape. The result, volatilization of flammable oils in tree needles which suddenly ignite in an explosion to create a catastrophic crown fire. This phemonenon was precisely the cause of conflagration fire in Mitchell Creek during those terrible Wenatchee, Washington, fires of 1970. Mitchell Creek is primarily mixed conifer/pinegrass. It was totally consumed by fire.

SUMMARY

Interpreatation of underburning effects in mixed conifer/pinegrass vegetation of the Blue Mountains in eastern Oregon suggest that: underburning occurred at about 10-year intervals; ponderosa pine is being replaced by Douglas-fir and white fir; ponderosa pine stands did not develop according to the "normal stand development" concept; stocking level control is required to avoid stagnation; range grasses decrease with increasing tree cover as pine is replaced by fir regardless of livestock use, thereby complicating interpretation of range trend; range condition guides can not be based on climax, instead they must be tied to tree crown cover in successional stands; pinegrass is capable of sustaining livestock use because it developed under periodic 100 percent use by fire; livestock are filling a large animal "niche" unoccupied by wildlife and account for as much animal production as all the deer and elk in the Blue Mountains: some plants seem dependent on fire for their survival, such as ceanothus and some legumes; species diversity, both plant and animal, is greater in successional pin-fir/pinegrass that in climax; use of climax for ecological interpretation seems tenuous since most stands have never been in a non-fire climax; soils developed under periodic fire and should be considered "brown forest" rather than "podzolic"; burning apparently does not damage soils since total herbage production is always greater following fire; underburning has influenced wildlife, such as the pileated woodpecker, in which successional trees were encouraged and stocking level control was maintained to produce large diameter trees; and fire hazard is changing from light, flashy fuel under open tree canopy to heavy fuels under a nearly closed canopy.

Control of underburning in the mixed conifer/pinegrass community has created an increased fire hazard in a known fire environment. We have changed from a fire-resistant plant community to a fire-susceptable plant community. We may NOT be able to manage for fir in this environment due to fire hazard. We may not have a choice about burning -- only a choice of how to burn: prescribed fire or wildfire.

SPECIES LIST

PLANTS

Arnica	Arnica cordifolia
Balsam woollyweed	Hieracium scouleri
Ceanothus	Ceanothus species
Douglas-fir	Pseudotsuga menziesii
Elk sedge	Carex geyeri
Firs	Abies grandis and Pseudotsuga menziesii
Heartleaf arnica	Arnica cordifolia
Lodgepole pine	Pinus contorta
Lupines	Lupinus spp.
Mixed conifer	Pinus ponderosa, Pseudotsuga menziesii, Abies grandis
Norway spruce	Picea excelsa
Pinegrass	Calamagrostis rubescens
Ponderosa pine	Pinus ponderosa
Strawberry	Frageria species
Vetch	Vicia americana
Western larch	Larix occidentalis
White fir	Abies grandis

ANIMALS

Deer	Odocoileus hemionus
Rock Mountain Elk	Cervus canadensis
Pileated woodpecker	Dryocopus pileatus

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Fire History, Junipero Serra Park, Central Coastal California[1]

James R. Griffin and Steven N. Talley[2]

Abstract.--Fire scars were analyzed on 11 trees from six plots in a small disjunct Pinus lambertiana forest in the Santa Lucia Range. Between 1640 and 1907 the frequency of fires hot enough to produce basal scars on the pines averaged 21 years. Excepting two lightning fires that were quickly extinguished, no fires occurred after 1907 until a lightning fire burned the entire forest in 1977. This was the most intense burn recorded within the life of the present forest.

INTRODUCTION

The highest point (1,788 m) in the Santa Lucia Range and adjacent mountains of central coastal California is Junipero Serra Peak (Griffin 1975). A small sugar pine (Pinus lambertiana) forest covers about 150 ha on the peak's north slope. The Junipero Serra Peak forest and a larger sugar pine forest on nearby Cone Peak are separated from the next sugar pine stands by 220 km (Griffin and Critchfield 1972). A large area of scrubby mixed hardwood forest and chaparral surrounds these disjunct pine forests. The Junipero Serra Peak forest is within a small unit of the Ventana Wilderness, Los Padres National Forest.

As part of a general ecological survey, we started floristic, stand structure, and limited fire scar dating studies on Junipero Serra Peak in 1975. In 1977 a lightning fire burned through the forest, but the next year we relocated the plots and continued work in the burn. Early results and some management implications have been reported (Talley and Griffin 1980); here only the fire history aspects of the study are given. Although the study was not designed for detailed fire frequency analysis, it does offer some information in a region where very little is known of fire history in montane pine forests.

METHODS

Thirteen 0.07 ha stand structure plots were located in 1975 throughout the entire range of pine forest diversity on the peak. Old sugar pines with large catfaces grew on or immediately adjacent to six of the plots. Fire scars on these trees were dated approximately in 1975. After the 1977 fire the same catfaces were studied in greater detail and several trees were added for a total of 11 catfaces.

Due to physical problems in using chain saws in rugged terrain with poor access and also administrative problems in using power tools within a wilderness, only minimum-sized fire scar sections were removed by hand saw from these trees.

A helicopter fire crew fell three 1977 fire-killed sugar pines on the wilderness boundary for us. Study of diameter growth rates and details of fire scar patterns on these stumps helped us to interpret the plot materials. Steven Talley developed the final fire scar chronology.

RESULTS AND DISCUSSION

Poverty of Cultural Records

Fires scarring old pines on Junipero Serra Peak span the Indian (before 1800), Spanish-Mexican (1800-1847), American settlement (1848-1906), and U.S. Forest Service (since 1907) land management eras. Through all four periods both humans and lightning storms started fires on the peak or close enough to reach the pine forest during hazardous fire periods.

We know little about Indian burning practice in this region. Burcham (1959) doubted that the local Indians burned chaparral or forest vegetati in the interior of the Santa Lucia Range. But burning in grassland and oak woodland has been documented (Gordon 1977). Even if forest burning were uncommon, Indian fires in grass or woodland could have traveled long distances to the peak. We do know that there was considerable historic and prehistoric Indian activity near the southern base of the peak.

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[1] Paper presented at the Fire History Workshop. [Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980].

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We have few additional facts on local burning practices by either the Spanish, Mexican, or early American ranchers. Conflicting view on whether these settlers started more or less fires than the Indians exist. By the 1890's a few reliable reports of large fires in the Santa Lucia Range began to appear (Talley and Griffin 1980). During high danger periods, some uncontrolled fires burned for many weeks; an October, 1906 fire covered some 55,000 ha.

Minimal Lightning Records

Lightning frequency is far lower in the Santa Lucia Range than in the higher southern California ranges or the Sierra Nevada. For example, Mt. Pinos (260 km southeast, up to 900 m higher than Junipero Serra Peak) may receive 100 lightning strikes per storm, 600 strikes per season (Vogl and Miller 1968). About one-third of the pines which Vogl and Miller sampled on Mt. Pinos had lightning damage. That degree of damage is not apparent anywhere in the Santa Lucia Range. On Junipero Serra Peak lightning-damaged pines are uncommon; only three were noticed near the plots.

Even though the lightning frequency is relatively low in the Santa Lucia Range, late summer or fall sub-tropical storms can start large numbers of fires across the region. But reliable records are too short-term and too incomplete to suggest regional patterns or long-term trends in frequency of lightning strikes. Only partial fire records exist for the Monterey District, Los Padres National Forest before 1919. The 1919-1931 records are still rather incomplete, and even the 1931-1977 offical count of 39 lightning fires does not reflect all the lightning fires actually suppressed in the Monterey District.

Historic Fires on the Peak

The first historic report[3] of a fire on the summit of Junipero Serra Peak was in 1901 when a blaze covered most of the mountain including the pine forest. No other fires started on the peak or traveled to the peak until September, 1939, when lightning started a fire in oak scrub on the northwest ridge. That fire was extinguished while still small. Lightning started a fire in pine forest on the north slope in September, 1959; it was also quickly suppressed. Two man-caused fires burned up the south slope but were controlled before reaching the pine forest: a 1,300-ha fire started by a vehicle in June, 1968; and a 2,500-ha fire started at a campground in May, 1976.

In August, 1977, following two seasons of serious drought, four lightning fires started in the Ventana Wilderness. They soon merged to form the "Marble-Cone" conflagration, which covered 72,000 ha. After burning for a week this fire reached Junipero Serra Peak and burned the pine forest. This severe surface fire (locally a crown fire) was probably the most intensive burn to occur within the life of the present forest. Numerous sugar pines that had received no serious fire damage during the preceeding 300 years were killed or severely damaged. Some of the catfaces studied in 1975 were burned so deeply that old fire scars were removed.

Fire Scar Frequency

The extreme intervals between fire scars on individual plots ranged from 4 to 108 years (table 1). Eleven of these fires were either spot fires

Table 1.--Estimated dates of fires scarring sugar pines on or adjacent to the Junipero Serra Peak plots. Dates within a given row are believed to represent the same fire. Trees per plot shown under plot number.

Plot 3 (1)	Plot 5 (2)	Plot 6 (1)	Plot 8 (3)	Plot 10 (2)	Plot 12 (2)
1977	1977	1977	1977	1977	1977
	1959				
1901	1901	1901	1901	1901	1901
	1896				1896
	1872	1872	1872	1872	1872
	1852	1853		1852	
	1840	1842	1842	1845	1843
	1820	1826	1826	1826	1825
					1812
		1809			
		1801			
1793	1791	1795	1795	1795	
	1786				
	1758	1757		1759	
				1755	
1743	1746				
	1740	1734		1739	
	1724	1717		1722	
		1707			
		1700			
	1688	1683			
		1668		1671	
		1664			
		1651			
		1640			

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[3] Plummer, F. C., and M. G. Gowsell. 1905. Forest conditions in the Monterey Forest Reserve, California. Unpublished report. [On file Los Padres National Forest, Goleta, California.]

or else not hot enough to scar trees on several plots. Over the entire time period the average interval between scars on a given plot ranged from 19 to 78 years. We emphasize that our sampling methods give us a conservative estimate of the total number of fires, particularly light fires early in the history of the forest.

Primitive fire control started in 1907. Before that time 13 fires scarred trees on two or more plots with an average interval between multiplot fires of 21 years (table 1). These fires probably lightly burned sizeable portions of this small forest.

Before fire control the study tree at plot 6 was scarred at least 18 times with an average interval of 15 years. Careful study of a complete catface section from this tree would probably reveal additional scars (but even with permission to use a chain saw, a prudent researcher would not saw very much on this hazardous snag).

A large proportion of the short fire intervals (10 years or less) occurred early in the record; eight before 1809, two after 1809. A decline in lightning frequency would help to explain such a trend. But if the Indians started more fires than the Spanish or Mexican settlers, a more likely cause of less frequent fires could be the complete destruction of the Indian culture near the peak soon after 1800.

The only other study which approaches ours in terms of vegetation type, topographic setting, climate, and cultural history was a brief survey on Big Pine Mountain, Los Padres National Forest (230 km southeast, up to 250 m higher than Junipero Serra Peak).[4] Although sample sizes were small in both studies, the results suggest similarities in fire history. One tree in the Big Pine Mountain study (resembling the tree on plot 6, table 1) was very sensitive to fire and had burned 17 times since 1651. This Big Pine Mountain tree averaged 12 years between fire scars during the Indian era prior to 1806. The shortest fire scar interval on any Big Pine Mountain tree was six years. The Big Pine Mountain forest last burned in a lightning fire in 1921.

CONCLUSIONS

This study adds a central coast example to the growing body of evidence that pre-Spanish fires were relatively frequent in California and that fire control during this century has contributed to less frequent but more severe fires. Although prescribed burning is increasingly suggested as a solution to fuel accumulation problems, prescribed burning in this region will be controversial, hazardous, and expensive. Prescribed burns will be particularly difficult in the isolated pine forests within chaparral regions that have wilderness status. The pine forests on Junipero Serra Peak, Cone Peak, and Big Pine Mountain well illustrate the situation in which serious administrative and emotional problems will arise with any fuel management program -- in addition to the normal difficulties.

As more data on fire history become available, implementation of effective prescribed burning programs in such areas will become more likely. It is desirable that more definitive dating of pre-fire control and especially pre-Spanish fire scars be done on the Junipero Serra Peak sugar pines. It is even more desirable that the abundant fire scars be studied in the Cone Peak forest. Cone Peak has a greater number of sugar pines of similar sizes and ages in a more mesic habitat. Portions of the Cone Peak forest are scheduled to become a Research Natural area, making it a very appropriate site.

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Land Use and Fire History in the Mountains of Southern California[1]

Joe R. McBride and Diana F. Jacobs[2]

Fire frequencies are related to periods of land use in the mountains of Southern California. Differences in fire frequencies were found for coastal sage scrub, chaparral, and yellow pine forest types between various sets of the Native American, Spanish-Mexican, American Pioneer, and Modern American land use periods. Analysis of fire maps was employed in the scrub; ring counts were used between fire scars in the forest types.

The mountains of southern California have experienced recurring wild fire for a very long time. The flora exhibits a variety adaptations indicating an evolutionary history in which fire was a major selective force. Man has been probably present in southern California for at least 11,000 years. His use of fire during this period has influenced the frequency of wild fires. Knowledge of fire frequency and its relation to land use history is prerequisite to understanding and properly managing vegetation. The objective of this paper is to investigate the relationship between land use and the frequencies of wild fires occurring in four major vegetation types in the mountains of southern California.

The Setting

The mountains of southern California occur in four landform provinces: the Transverse Ranges, Peninsular Ranges, Mojave Desert, and Colorado Desert. Only mountains in the Transverse and Peninsular Ranges support coniferous forests of commercial value or dense scrub-dominated vegetation which presents a significant fire hazard. This paper discusses studies made in the Transverse Ranges.

The Transverse Ranges are oriented along east-west axes from Santa Barbara to San Bernardino. The vegetation varies along altitudinal gradients with the following sequence of types moving upon the seaward side: coastal sage scrub, chaparral, oak woodland, yellow pine forest, fir forest. On the desert side the vegetation shows the influence of lower precipitation with a pinyon-juniper woodland followed by a high desert scrub community occurring at lower elevations in place of the coastal sage scrub.

Fire history investigations were conducted in the coastal sage scrub, chaparral, and yellow pine forest types. These types were selected because they present major problems of fire control and management.

The coastal sage scrub occurs from sea level to about 1000 m. The type is common on sites that are climatically or edaphically dry. Rainfall is 40-80 cm annually. The dominants in this type are *Artemisia californica* (coast sagebrush), *Salvia apiana* (white sage), *S. mellifera* (black sage), *S. leucophylla* (purple sage), *Eriogonum fasciculatum* (California buckwheat), *Rhus integrifolia* (lemonade-berry), and *Encelia californica* (California encelia). These soft shrubs form a generally discontinuous cover .5 to 1.5 m tall.

Chaparral is found from 300 to 1500 m on the more rainy coastal sides of the mountains and from 1000 to 1600 m on interior sides. Average annual rainfall ranges from 55 to 100 cm. Species composition varies throughout the type. *Adenostema fasciculatum* (chamise), is common and often dominant. Co-dominants may be species of *Arctostophylos* (manzanitas), *Ceanothus* (ceanothus), *Heteromeles* (toyon), *Rhus* (sumacs), and *Quercus* (oaks). These hard shrubs form a complete crown canopy 1 to 3 m in height.

The yellow pine forest dominates above the chaparral on the higher mountains between 2000 and 2700 m. On north-facing slopes it may be found in

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favorable canyons below 1300 m; on south-facing slopes it is usually first encountered above 1600 m. It occupies a variety sites and may be locally replaced by chaparral on shallow soil on south-facing slopes or by riparian species in areas of saturated soil. Species composition varies with altitude. *Pinus ponderosa* (ponderosa pine) and *Quercus kelloggii* (California black oak) dominate at lower elevations while *Pinus Jeffreyi* (Jeffrey pine) and *Abies concolor* (white fir) dominate higher up. The yellow pine forest type was divided in this study into a ponderosa pine type and a Jeffrey pine type.

History of Land Use

The history of land use in the Transverse Ranges can be divided into four periods: Native American, Spanish-Mexican, American Pioneer, and Modern American. Land use in the Native American period was characterized by hunting and gathering. Ethnographic information indicates that Native Americans used fire as a management tool to facilitate both hunting and gathering of certain plant materials (Lewis, 1973). Fires were set annually in lower elevation grasslands and some chaparral areas were periodically burned in the fall (Aschmann, 1959). The major concentrations of Native Americans were along the coast and in lower elevation valleys. They traveled into the mountains annually to collect acorns and pine seeds in the autumn, and occasionally to hunt.

The Spanish-Mexican period can be characterized as a period of livestock grazing. It began in 1769 with the establishment of the first mission. Spanish and later Mexican land grants divided up the lower elevation into ranchos where large herds of cattle were raised for hides. Conflicts arose between the early Spanish settlers and the Native Americans over burning of grassland at lower elevations. The Spanish were dependent upon these grasslands for winter range; the Native Americans were dependent on these same grasslands for root and bulb crops which they collected annually after burning the grass. The Spanish stopped the burning and the Native Americans were removed from the grasslands. The higher elevation coniferous forests were generally not utilized by Spaniards or Mexicans for grazing.

The Spanish-Mexican period ended in 1848 when the United States took possession of California from Mexico. In the same year gold was discovered in California. American prospectors explored not only the Sierra Nevada, but the mountains of southern California too. Significant lodes were discovered at higher elevations in the Transverse Ranges. Mining towns sprang up overnight. Fire was a constant threat to these crudely constructed towns and many were burned to the ground more than once in their brief lifespans. Many of these fires spread into adjacent forests. When the gold was depleted these towns were abandoned and much of the mining population shifted to the lower elevation valleys to farm. A few stayed behind to develop sawmills and a timber industry. Others had ranches at lower elevations and returned to the mountains for summer grazing of both sheep and cattle. Coniferous zones of the San Bernardino Mountains were often used for summer grazing. Sheep herders commonly set fires in mountain meadows at the end of each grazing season to improve forage the following year. It was common practice among the early lumbermen to burn slash which interfered with log extraction, and sawmill fires were another common source of wild fire (Johanneck, 1975).

The exploitation of resources through mining, logging, and livestock grazing was curtailed in the 1890's with the establishment of federal forest reserves. The year 1905 was the beginning of a new period in which conservation practices controlled land use. In 1905 the Forest Reserves were transferred from the Department of the Interior to the newly formed U.S. Forest Service. In the same year California enacted the Forest Protection Act which provided for fire control on private lands. These events resulted in the elimination of broadscale burning for range and initiated a regulation of forest harvesting. Since 1905 land use has shifted from logging and grazing to recreation and watershed protection.

Fire History in Coastal Sage Scrub and Chaparral

The Santa Monica Mountains, west of Los Angeles, were selected for studying fire history in the coastal sage scrub and chaparral. These mountains lie near the western end of the Transverse Ranges and rise from sea level to an elevation of 945. The vegetation is composed of (1) grassland occurring along coastal terraces and at lower elevations at the northern base of the mountains, (2) coastal sage scrub extending from sea level on mountain slopes, or at the base of slopes behind the coastal terraces to elevations of about 330 m on the seaward side (south) and from elevations of 150 to 350 m on the interior (north) side of the mountains, and (3) chaparral occurring at elevations above the coastal sage scrub. Minor areas of oak woodland occur along streams.

An analysis of historic fires was used to determine frequencies of fire in the coastal sage scrub and chaparral of the Santa Monica Mountains. Maps of areas burned in these mountains from 1909 to 1977, compiled by the Division of Forestry of the Los Angeles County Fire Department, were used to determine fire frequencies. These maps recorded all fires over 0.1 ha (Class B and larger).

Two hundred eighty-one sample plots, each with an area of 4 ha, were located at random within the areas dominated by coastal sage scrub and chaparral on U.S.G.S. topographic maps. The plots were divided between the two vegetation types to give a 3% sample of the area in each type. These plot maps were compared with the fire history maps and each fire which had burned at least one-half

any plot was tallied as a fire event in that
lot. This procedure was adopted to minimize the
rror associated with transferring fire boundaries
rom Los Angeles County Fire Department Maps
which had been drawn at various scales) to the
.S.G.S. maps. The number of fires on each plot
as divided into the time period covered by the
aps (68 years) to determine the intervals between
ires. Average intervals were determined for the
lots in each vegetation type.

The average interval between fires was 14
ears for the coastal sage scrub and 16 years for
he chaparral. These averages are significantly
fferent at the .05% level. The difference in
re frequencies between the two types may be due
differences in access, temperature, and rate
recovery following fire of shrub species in the
o types. Access to the coastal sage scrub is
etter than to the chaparral. There is a greater
nsity of roads and houses in the coastal sage
rub than chaparral. Opportunities for accidental
well as arson fires are, therefore, considered
eater. Temperature gradients result in higher
mmer and fall temperatures in the lower elevation
astal sage scrub than in the chaparral. This
fference increases the number of days during the
ar when fires can readily be ignited in the
astal sage scrub. Recovery of crown canopies
llowing burning is more rapid among the coastal
ge scrub species than in the chaparral species.
anes, 1971). This more rapid rate of recovery
the part of the coastal sage scrub may result
an earlier reestablishment of the fuel con-
nuity necessary to carry fire.

The fire intervals of 14 and 16 years rep-
sent the intervals occurring in the modern
erican period of land use. An interval of from
to 10 years has been suggested for coastal sage
rub in the San Gabriel and San Bernardino
untains for the same period by Hanes (1971).
ilpot (1973) proposed intervals of 15 to 17 years
r chaparral in the San Bernardino Mountains. In
is modern American period man has acted both as
e principal agent of fire ignition and as the
ntrol. In earlier periods of land use man was
so the primary cause of fires at lower elevations,
t it is unlikely that man's influence was as
portant in the higher elevation stands of
aparral in the Santa Monica Mountains. These
aparral stands were of little value for grazing
ring the American Pioneer and Spanish-Mexican
riods. Sauer (1977) reports that unlike many
tive American tribes in southern California, the
umash living in the Santa Monica Mountains did
t burn vegetation in their management of the
nd. Fire ignition may have resulted as a result
carelessness with campfires, but the major cause
fire during this period was from lightning.
ghtning is infrequent in the Santa Monica
untains but is the cause of occasional fires.
gl (1976) has suggested a fire frequency of 20
ars for lightning caused fires in chaparral during
e-historic times. A similar interval has been
oposed by Aschman (1976) for pre-historic chapar-
l fires in those regions where burning was not
practiced by Native Americans. This suggests that a reduction has occurred in the interval between fires in the Santa Monica Mountains, when one contrasts the Native American period with the modern American period. Information on the fire history of both the Spanish-Mexican period and American Pioneer periods is unfortunately limited.

Fire History in Ponderosa and Jeffrey Pine Forests

The San Bernardino Mountains, near the eastern end of the Transverse Ranges, were used as a location to study fire history in the ponderosa and Jeffrey pine forest types. The San Bernardino Mountains range in elevation from about 400 m to 3,500 m. Coniferous forests found at elevations above 1500 m. Ponderosa pine dominates the somewhat lower elevations of southern and western portions in this zone, while Jeffrey pine dominates the higher elevations to the north and east. The ponderosa pine forest is contiguous with either chaparral or oak woodland types at its lower edge. The lower elevations at the northern and eastern boundaries of the Jeffrey pine forest are bordered by pinyon-juniper woodlands.

Fire frequency was determined by counting annual rings between fire scars on wood sections removed from the base of living trees. Twenty-nine ponderosa and 38 Jeffrey pines were sampled. Trees were selected over the entire range of each forest type. A minimum distance of 1.6 kilometers was maintained between any two trees selected for sampling. A tree was considered for selection only if one or more trees within 100 m had similar fire scars. Some inaccuracy in dating by this method can be expected because of the possible occurrence of missing rings. Cross dating of rings was not possible because of the distortion of ring widths in the healed over portions of the small wood samples. Removal of larger wood sections would have resulted tree mortality.

Average intervals between fires were determined for three periods in each forest type. These periods were (1) prior to 1860, (2) 1860 to 1904, and (3) 1905 to 1974. They correspond to the Native American, American Pioneer, and Modern American periods of land use. Those fires prior to 1860 can be used to characterize the Native Amercan period because neither the Spanish nor the Mexican settlers used the ponderosa or Jeffrey pine forests of the San Bernardino Mountains. However, the population of the major tribe using the pine forest of the San Bernardino Mountains was reduced about 50% during the Spanish/Mexican period (Bean, 1978). Use of these mountains by Native Americans was further reduced in 1852 when American pioneers constructed a road into the mountains. By 1860 the American pioneers had essentially eliminated the Native Americans.

The fire intervals for each period are shown in Table 1. Analysis of these data shows significant differences at the .05% level between the period from 1905 to 1974 and the earlier periods within each species. No significant differences were found between the period prior to 1860 and the period from 1860 to 1904 for either species. There was a significant difference between the two species for the modern period, 1905 to 1975. No significant difference occurred between the two types prior to 1905.

Table 1.--Average interval between fires in ponderosa and Jeffrey pine forests of the San Bernardino Mountains.

	Interval between fires (yrs)		
Forest Type	Prior to 1860	1860 to 1904	1905 to 1974
Ponderosa pine	10	14	32
Jeffrey pine	14	19	66

The fire frequencies determined in ponderosa and Jeffrey pine forests in the Native American period reflects ignitions by the Cahuillas and by lightning. The Cahuilla-caused fires were usually set in meadows within the forests or in the chaparral. Some of these fires burned into adjacent forest stands. Fires set in the chaparral may have played a significant role in igniting the lower elevation coniferous stands. The distribution of chaparral, oak woodland, and coniferous forest species at the interface between the chaparral and yellow pine forest in the San Bernardino Mountains has been interpreted by Minnich (1977) as a pattern controlled by fires moving up from the lower elevations of the chaparral. Lightning was the common cause of fire ignition in the higher elevations of the Jeffrey pine forest. The Native Americans made limited use of these higher elevation forest stands and a less frequent interface occurs between Jeffrey pine stands and chaparral.

The fire frequencies calculated for the American pioneer period in both the ponderosa pine and Jeffrey pine forest types do not differ significantly from frequencies in the Native American period. It is assumed that the pioneer miners, sheep herders, ranchers, and lumbermen replaced the Native American as causal agents for wildfires. The elimination of the Native Americans from the mountains did not result in a significant increase in the interval between fires as has been reported for the Sequoia-Kings Canyon region of the Sierra Nevada by Kilgore and Taylor (1979).

The activities of the American pioneers may have resulted in more fires actually having been set, purposefully or by accident, in the forests themselves. The use of fire by stockmen, which was considered a serious threat to the forests, was a major impetus for the establishment of a federal forest reserve in the San Bernardino Mountains.

The significant increase in the length of interval between fires in the Modern American period is a result of fire control activities by the U.S. Forest Service and the California Division of Forestry. These activities included the prevention of burning by stockmen and the enforcement of fire safety regulations at sawmills and lumber camps. Advancements in fire suppression technolog have allowed for a more rapid control of fires, thus reducing the average extent of individual fires. As the area of forest burned has decreased since fire records have been maintained, the numbe of fires have increased (U.S.F.S., 1940-79). Lightning has accounted for about 33% of all fires during the last twenty years. Fires initiated in the chaparral continue to be a source of ignition for fires in the yellow pine forest. In the more recent part of the Modern American period, recreation has replaced grazing and lumbering as the principal land use in the conifer forests of the San Bernardino Mountains. The long term impact of this land use is yet to be determined.

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Fire History in the Yellow Pine Forest of Kings Canyon National Park[1]

Thomas E. Warner[2]

Abstract.--Preliminary results of an on-going fire scar study in the yellow pine forest of Kings Canyon National Park indicate a mean fire frequency per individual tree of approximately 11 years for the period 1775 until 1909, the date of the last recorded fire scar on sampled trees. For the entire area sampled (approximately 400 acres) there was a fire on an average of once every 3.5 years.

INTRODUCTION

Cooper (1960), and Weaver (1951, 1959, 1961) ave discussed fire in terms of its ecological ole in the ponderosa pine type. Other authors Wagener, 1961; and McBride and Laven, 1976) have resented fire frequency data for yellow pine orests in the central and northern Sierra Nevada nd San Bernardino mountains respectively. ilgore and Taylor (1979) have reported on the esults of extensive fire scar analyses in a equoia-mixed conifer forest in the southern ierra Nevada. Their work was at elevations of 500-7000 feet (1675-2135 m) in mixed stands that ncluded a relatively small proportion of sample rees in the ponderosa pine type. Other recent tudies (Parsons and Hedlund 1979; and Pitcher 980) have addressed the fire frequency question n the foothill and upper montane zones espectively in Sequoia National Park, but no ork to date has been reported on fire frequency n the lower montane pine type in the southern ierra Nevada.

The purpose of this paper is to present reliminary results of a study initiated in 1980 o determine fire frequency in the lower montane ellow pine forest of Kings Canyon National Park. he results of this study, will be utilized by ark Service resource managers in establishing he periodicity of prescribed burning in this egetation type in the Parks.

STUDY AREA

The study area (fig. 1) is located at approximately 37° latitude in the U-shaped glacial valley of the South Fork of the Kings River in Kings Canyon National Park. This area is about 7-3/4 miles (12 km) long by 1/4 to 1/2 (0.4-0.8 km) mile wide and encompasses about 1600 acres (650 ha), extending from Lewis Creek on the west to Copper Creek on the east. Elevations range from 4500 feet (1370 m) in the west to 5000 feet (1525 m) in the east. The results reported in the paper are from approximately 400 acres (160 ha) in the west end of the valley.

The western portion of the study area was last glaciated during the Pleistocene epoch about 75,000 years ago. The eastern portion from about 1000 feet (350 m) east of the Cedar Grove Ranger Station in Camp 3, was more recently glaciated about 45,000 years ago (Birman 1962).

Soil in the study area is generally a sand or sandy loam of granitic origin, of medium, 13-32 inches (33-81 cm) depth, and with a low water holding capacity (Sellers 1970).

Climatic data for Cedar Grove is limited. Munz (1973) presents a general range of annual precipitation for the yellow pine community in California of 25-80 inches (64-203 cm). Grant Grove, located at an elevation of 6600 feet (2010 m), 15 miles from the study site, receives an average of 42 inches (106 cm) precipitation annually. Most of the precipitation in Cedar Grove is as rain from October through April.

The vegetation is predominantly a ponderosa pine forest comprised of ponderosa (*Pinus ponderosa*) and Jeffrey pine (*P. jeffreyi*) (Hammon, Jensen and Wallen 1971). Two other important species in this type are incense cedar (*Calocedrus decurrens*), which is about co-equal with pine in abundance (Sellers 1970) and California black oak (*Quercus kelloggii*). Sugar pine (*Pinus lambertiana*) is a less common associate. Most stands are uneven-aged

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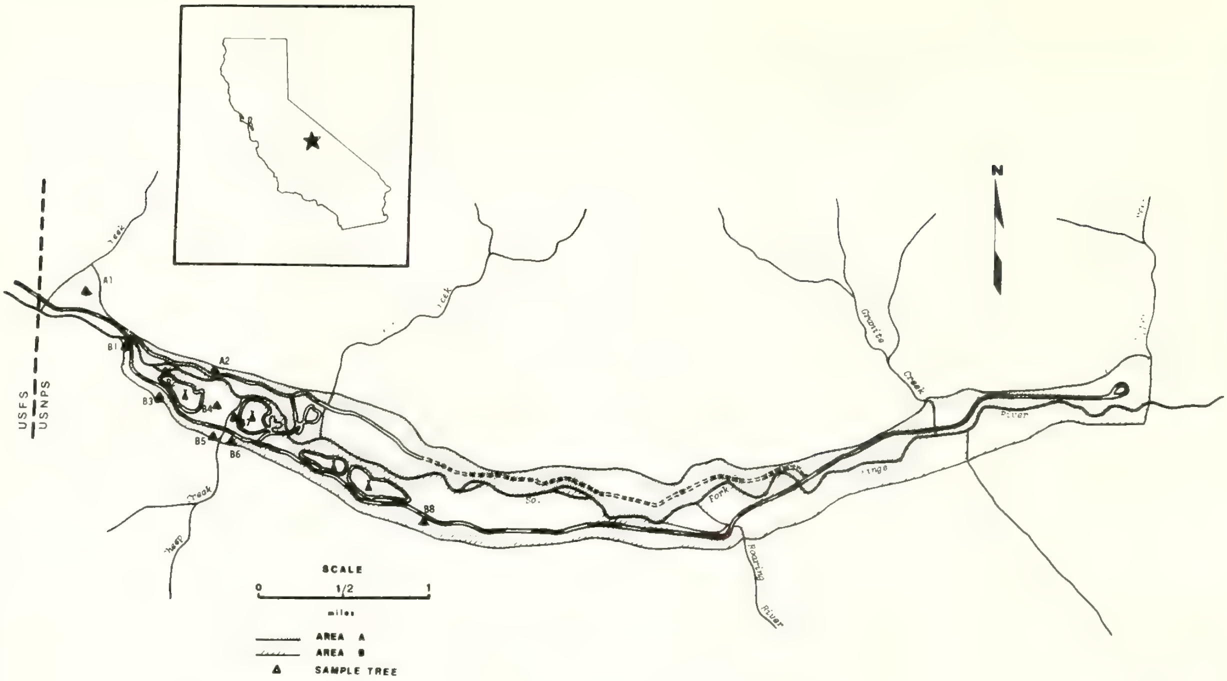

Fig. 1.-- Cedar Grove fire history study area, showing location of sample trees.

with total crown cover variable, from 10-100%. Sellers (1970) reports basal areas ranging from 115-750 ft^2/acre (27-171 m^2/ha), with a modal value of about 200 ft^2/acre (46 m^2/ha). Ages for 36-48 inch (91-122 cm) diameter ponderosa pine are typically 250-300 years, while those for sugar pine greater than 48 inches (122 cm) diameter are 350-400 years. Sellers (1970) found 24-36 inch (61-97 cm) incense cedar to be 155-240 years old and 16-25 inch (41-64 cm) black oak to be 160-270 years old.

The other main vegetation type is lower elevation pine-fir (Hammon, Jensen, and Wallen 1971). This is comprised of the same species as above except with the replacement of black oak by white fir (Abies concolor). This type is most commonly associated with more mesic sites adjacent to the river.

Another important species which occurs locally on xeric glacial morraines in the valley and comprises much of the hardwood type on the canyon walls is canyon live oak (Quercus chrysolepis). Associated species in the latter type are Arctostaphylos mariposa and Cercocarpus betuloides.

METHODS

This study was patterned after the guidelines in Arno and Sneck (1977). Reconnaissance transects were systemtically laid out at approximately 1/4 mile (0.16 km) intervals beginning at the west end of the study area. These transects are oriented north-south and are confined to the pine type on the valley floor. Where the pine type extends up the south wall of the canyon the transects were terminated at an arbitrary pre-determined distance of 330 feet (100 m) from the road. All fire-scarre trees encountered in a 66 foot (20 m) wide search strip each side of the transect were tagged for future reference, mapped and recorded. Upon completion of the transect the tree with the greatest number of scars was selected for sampling Also included in the sample were three previously collected fire-scarred cross sections from bark beetle killed trees whose locations coincided with the sample area.

The sampling method followed that of McBride and Laven (1976). After drying for a week or two, the wood sections were sanded with a belt sander, first with coarse (40 grit) and then with a fine (100 grit) belt. The rings were counted and every tenth ring, starting from the cambium, and every fire scar were marked. Wetting the section facilitated counting. For counting very closely spaced annual rings a 7X to 30X variable power binocular microscope was used. The number of year back to the first scar and the interval between ea previous fire was recorded. Then these dates were plotted on graph paper and some of the years were adjusted to correlate the chronology as described by Arno and Sneck (1977). Finally a mean fire frequency for the entire area was calculated. In addition, a combined mean fire frequency per individual tree was also calculated. The time period under consideration was from 1775, the date there was a minimum of 4 fire-scarred sample trees in the area, until 1909, the date of the last recorded fire scar on sample trees.

RESULTS

During the 134 year period from 1775 to 1909 a fire burned somewhere within the approximately 400 acre (160 ha) portion of the study area sampled on an average of once every 3.5 years. This is compared to a mean frequency per individual tree of once every 11.4 years for pine after initial scarring. Incense cedar did not seem to be as reliable an indicator of fire, even after it was initially scarred, as was pine. For this reason, cedars were not included in the individual frequency determinations. The last recorded fire scar on any tree in the sample area was in 1909. These figures are based on a very limited sample of only ten trees which recorded a total of sixty-five individual fires during this period. This corresponded to an estimated 38 separate fire-years after adjustment of the master chronology. Several trees exhibited multiple scarring (fig. 2), four contained nine or more scars.

DISCUSSION

Two factors, soil moisture availability and fire have been cited as being the most important in determining the composition and structure of the ponderosa pine forest (Rundel et al. 1977). Sellers (1970) noted a correlation between height above the river and species distribution. Black oak and ponderosa pine tend to increase towards the xeric end of the moisture gradient while the converse is true for incense cedar and white fir. Sugar pine is intermediate in moisture stress tolerance, but tends to decrease with increasing elevation above the river.

Fire frequency affects stand density which in turn influences species composition (Rundel et al. 1977). Ponderosa pine tends to increase with decreasing stand density. The same is true for black oak, which replaces pine on the more xeric sites. Incense cedar shows the reverse tendency while the distribution of sugar pine tends to be unrelated to stand density (Sellers 1970). Frequent light ground fires tend to favor shade intolerant species such as ponderosa pine and black oak and disfavor shade tolerants such as incense cedar and white fir. Fire exclusion then would tend to increase these latter species relative to the former. This is exactly what Sellers (1970) observed when he analyzed the size class distributions for these species. The ponderosa pine-incense cedar-black oak fire sub-climax is being replaced in the absence of fire by one in which white fir and sugar pine are assuming greater relative importance at the expense of black oak.

The results of this study, even though preliminary in nature, tend to support the successional observations by Sellers. Fire frequency apparently began to show a decrease about 1880 in the study area and came to an abrupt halt in 1909. This drastic alteration in the role of fire has led to changes involving species composition and stand structure in the climax community.

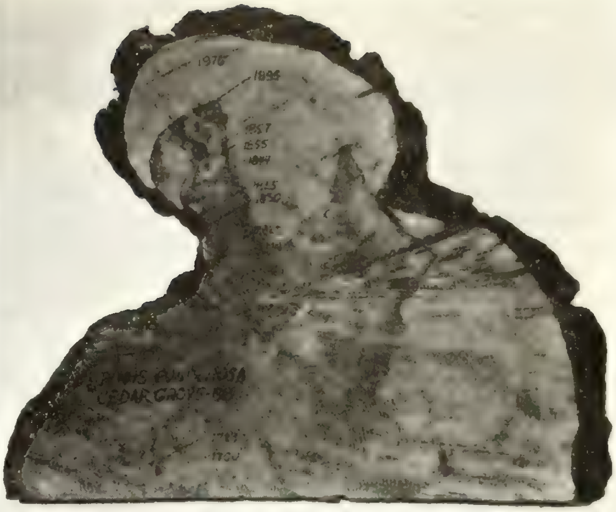

Fig. 2.-- Cross section of fire-scarred tree killed by bark beetles. This particular tree had recorded a total of 12 separate fires from 1721, when it was first scarred, until 1895. The tree was felled in 1977.

Exactly what influence aboriginal burning had on the fire frequency of Kings Canyon is uncertain.. What is known, however, is that intensive use of the Parks in general began about 1000 A.D. with the ancestors of the Monachi, or Western Mono Indians, and continued until shortly after white intrusion around 1850 (Elsasser 1972). This use was seasonal in nature and the total number of Indians in Kings Canyon during any one year was probably less than 100 (Sellers 1970). One particular village site, located in the study area, was apparently occupied from about 1350 to 1700 A.D. (Elsasser 1972)

Reynolds (1959) has documented the use of fire by Indians in the central Sierra Nevada to aid in acorn collection. While there is no positive evidence that the Wobonuch Monachi Indians in Kings Canyon burned periodically, the presence of bedrock mortars in the immediate vicinity indicates utilization of acorns as a food source and strongly suggests that they possibly did (Seller 1970).

Kilgore and Taylor (1979) compared contemporary lightning-caused fire frequency with that from fire scar records in their study area. They concluded that natural ignitions alone were insufficient to account for the observed historic fire frequency. This could only be explained by some other ignition source, namely Indians.

Apparently lightning caused fire ignitions on the valley floor of Kings Canyon are relatively rare; only seven were recorded in a 40 year period. (1940-79). This does not take into account, however, ignitions on the walls of the canyon, nor those either up or down canyon, which, had they not been suppressed, undoubtedly would have influenced the fire frequency in the valley. It is unlikely, though, that even taking into consideration the spread of some of these fires from outside into the area the resultant fire frequency would equal the historic fire frequency as determined from an analysis of fire scars. This then, would support the tentative conclusion that some other agent, most likely Indians, was at least partly responsible for the observed frequency.

Recognizing the effect of fire exclusion on vegetation and fuel conditions and realizing the need to reintroduce fire into the Parks' ecosystems has led to a program of prescribed burning in Sequoia and Kings Canyon. An intensification and extension of that program throughout the mixed conifer zone of the Parks since 1978 has resulted in approximately 300 acres being prescribe burned in Cedar Grove since that date.

Hopefully, the conclusion of this study will find us better able to describe present stand conditions in the yellow pine forest in terms of past fire frequecy and allow us to extrapolate that information to our present management programs.

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The Influence of Fire in Coast Redwood Forests[1]

Stephen D. Veirs, Jr.[2]

Abstract.--In its northern range redwood vegetation is influenced by fires of differing intensity. Relatively hot fires appear essential for the establishment of Douglas-fir (*Psuedotenga menziesii*) trees as discrete age classes. Coast redwood (*Sequoia sempervirens*) and several lesser associates are successful with or without fires. The effects of two fires are described.

INTRODUCTION

The influence of natural fire in old growth dwood forest is poorly understood. Redwood *equoia sempervirens*) stands have been described even-aged, (Cooper, 1965), and all-aged (Fritz, 29), a climax species (Weaver and Clements, 29) and as a subclimax, fire dependent species ooper, 1965, Stone et.al. 1969). Roy (1966) scribed fire as the worst enemy of redwood. A tter understanding of the role of natural fire redwood forest vegetation is necessary to guide ng-term management of old growth redwood forests w largely confined to parklands. Restoration or rpetuation of the natural processes which domine this and related vegetation types, or artifial management to mimic these processes depends on a better information base than is now availle. Research has been carried out in and near dwood National Park to gain needed information r management of this superlative natural ecostem. The results of part of this work (Veirs, 79) suggest that redwood maintains its dominant atus in the northern portion of its range with without the influence of fire. On the other nd, Douglas-fir (*Psuedotsuga menziesii*), the jor canopy associate of redwood, appears to cur only as discrete age classes of trees able 1.) established following fires.

In moist low elevation sites the return terval for fires which open the redwood canopy ough to allow Douglas-fir seedling establishment d survival may be as long as 500-600 years, on termediate sites from 150-200 years, and on high evation interior sites 33-50 year intervals. dwood stands are best developed where fire frequency and intensity is low. Greater fire frequency and intensity along with difficulties of seedling establishment appear to limit the inland development of redwood. Other lesser associates of redwood and Douglas-fir occurring in these forests; western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), and tan oak (*Lithocarpus densiflorus*) all, like redwood, appear to be successful in the presence or absence of fire.

Here I examine the relative impact of two fires on old growth redwood vegetation and subsequent tree establishment.

METHODS

Stand histories have been developed (Veirs, 1972, 1979) for several hectare plots by sampling before and after timber harvest. Tree species, density and ages were obtained directly and fire scars dated by growth ring counts. Data from one stand with a well-defined low intensity fire which occurred about 1880 is compared with data from stand burned in October, 1974. Mortality and establishment was determined by counting overstory trees and by systematic sampling of seedlings. Tree ages on the latter site are inferred from data available from a logged area nearby and from sections removed from fallen trees.

DESCRIPTION OF THE STUDY SITES

The 1880 fire site was located east of Crescent City, California in the Mill Creek basin. The area sampled (2.47 acres) was a moist west-facing slope, elevation 250-350 feet. The overstory was largely redwood with a few Douglas-fir and there was a dense understory of western hemlock with few plants in the herb layer. This fire may have been intentionally set by a prospecting landowner to expose the soil surface, or it may have occurred naturally.

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[1] Paper presented at the Fire History Workshop, aboratory of Tree Ring Research, University of izona, Tucson, Arizona, October 20-24, 1980).

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Table 1.--Age classes of Douglas-fir occurring in coastal redwood vegetation, Humboldt and Del Norte counties, California.

Location	Distance from Pacific Coast	Elevation	Aspect	Age Classes
	(miles)	(feet)	(Drection slope faces)	Years
Near Klamath River	1.2	800	Ridgetop	250
Near Klamath River	1.9	300-500	N	250
High Prairie Creek	2.8	1300-1500	SW	50,75,100,190
Mill Creek	3.0	250-350	WSW	575
Redwood Creek	5.0	600-800	SSW	200,275,350,450,575
Redwood Creek	5.4	600-800	WNW	400,550
Redwood Creek	5.9	700-900	W	300,400,500
Eel River (Fritz,1929)	---	---	---	150,300

At the time of sampling the overstory redwoods ranged in age from 400 to 1200 years, all the Douglas-fir were approximately 550 years old. The understory hemlocks comprised two distinct groups; a few older trees 180-220 years and many young trees all less than 93 years of age.

The 1974 fire site was located east of Orick, California in the Redwood Creek basin. The area burned was 6.0 acres on a moderately dry slope between 600-800 feet in elevation. The overstory was largely redwood with a few Douglas-fir; the redwoods ranging broadly in age from a few to 1450 years. The Douglas-fir are thought to be in two age classes between 200 and 400 years of age. The subcanopy and understory was largely hemlock with two probable age classes approximately 75 years and 200 years old. Tan oak and grand fir also occurred as associates. This fire was probably ignited accidently by forest workers falling nearby timber.

FIRE BEHAVIOR

While the time of year the 1880 fire burned is unknown, there is evidence to suggest that it occurred under conditions which yielded a low intensity fire. Hemlock, well-known for its sensitivity to fire, was not always killed. About five hemlock per acre survived (Table 2.). Several of these surviving hemlock displayed evidence of release following the fire; increased diameter growth rates were observed on survivors. The absence of deadfall, the presence of a largely intact canopy of old redwood and Douglas-fir (cover approximately 90%) and the absence of a well-defined scar record of the fire also suggests low intensity.

The 1974 fire may have been ignited in the afternoon or evening during the first week of October and was controlled after its discovery the following day, burning six acres. I was able to observe spread rates of approximately 2-3 ft. per minute down hill and slightly faster up hill with flame lengths of 0.5 to 2 feet. Flames reached the canopies of two or three redwoods and two Douglas-firs by burning up rifts and resin on the bark, but damage to living portions appeared limited. No crowning occurred. In spite of an extremely dry summer, low wind conditions and a slight inversion combined to yield a fire of relatively low intensity. Rain a few days later put out any smoldering materials including the aerial fires in stems.

RESULTS AND DISCUSSION

Following the 1880 fire, hemlock seedlings (Table 2.) became abundantly established forming a dense subcanopy which has limited the reestablishment of herbs, shrubs and trees to the present time. A few redwood also became established but none of these occurred on the sample site. The fire caused no significant changes in the canopy composition and the understory of hemlock may also have been essentially unchanged. The stand bore approximately one-half fire scar per overstory tree with no well-defined pattern over an average life of about 800 years. Clearly this mesic stand has had relatively little impact from fires during the past several hundred years. What will happen as the understory hemlocks mature and senesce and when overstory redwood and Douglas-fir mortality occurs remains to be seen.

The 1974 fire, in spite of its apparent low intensity caused complete mortality among the small and large hemlock alike, with relatively little mortality among all other tree species (Table 2.). Similarly, the strong establishment of hemlock, redwood and Douglas-fir seedlings is remarkably different from the 1880 fire. It is possible that the very dry conditions permitted more complete burning of duff and woody materials in which the hemlock were rooted. Whether the hemlock-redwood-Douglas-fir seedling establishment was a fortuitous accident or was due to the conditions of the burn is unknown. No estimates of light intensity have been made on the 1974 burn, however, the relatively high light requirement for Douglas-fir appears to have been met. Basal sprouting by tan oak and young redwood is typical

Table 2.--Tree survival, mortality, and establishment following two fires in redwood forest vegetation.

Species	Prefire trees/acre greater than 12" d.b.h.	Trees killed by fire/acre	Surviving trees or seedlings estab'd following fire/acre	Trees sprouting per acre
1880 FIRE				
Redwood	20	probably none	none	1
Douglas-fir	2	probably none	none	does not sprout
Western Hemlock	5 or more	possibly many	607	does not sprout
1974 FIRE				
Redwood	17	0.5	446	1.5(all free stand'g trees under 12" d.b.h.) (1.25 sprout groups/ acre associated with overstory trees also sprouted again.)
Douglas-fir	2.6	0.3	250	does not sprout
Grand fir	1.6	none	present but did not occur in sample plots.	does not sprout
Western hemlock	5.16	all	473	does not sprout
Tan oak	1.6	none	none	7 (including trees less than 12" d.b.h.)

for this site and may be of great importance in maintenance of these species in sites where regeneration from seed is strongly limited by climate conditions.

CONCLUSIONS

It is clear that much additional information is needed in order to clarify the role of fire in redwood vegetation. The infrequent establishment of the Douglas-fir component of moist site redwood stands is for now the most interesting aspect of the dynamics of old growth redwood vegetation. Additional observations of fires or experimental burning in this vegetation type, and extensive mapping of Douglas-fir age classes and old fire patterns is needed to clarify the natural role of fire in redwood vegetation. Once done, this information can be used to develop sensitive long-term management to ensure the perpetuation of dynamic old growth redwood forest ecosystems, in parks, if nowhere else.

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Forest Fire History Research in Ontario: A Problem Analysis[1]

Martin E. Alexander[2]

Abstract.--This paper surveys available information on fire regimes and methodology employed in elucidating these regimes during the suppression, presuppression and postglacial periods, principally in the boreal and Great Lakes-St. Lawrence forest regions of Ontario. The presettlement section reviews written accounts, tree-ring and fire scar dating, mapping of fire patterns, and stand age-class distribution. Research needs are suggested.

INTRODUCTION

Resource managers, recognizing that fire exclusion is often impractical and undesirable, and that total relaxation of fire protection cannot be tolerated, are faced with the formidable challenge of coming to terms with forest fires in land management. The first and most basic question that must be considered is: "What was the natural fire regime prior to the initiation of fire suppression?" An analysis of available information and data sources and a review of fire history methodology are logical steps in formulating a research program.

Heinselman[3] made the following statement about fire regimes which has served as a guiding principle in the preparation of this paper:

> ...there are a limited number of variables that determined the natural fire regimes of most regions, and of specific physiographic sites within regions. Once these variables are understood, and we have enough good fire histories to relate them to, it will become possible to estimate the probable natural fire regimes of most areas without additional fieldwork. Some of these variables include the climate of the area, the electrical storm occurrence rate, the known lightning-fire occurrence rate, the natural vegetation of the area, the productivity of the area, the natural balance between fuel accumulation and decay, the local soils and topographic situation, and any special information concerning possible unusual use of fire by man (in presettlement times).

Sharpe and Brodie (1931) remarked that "Throughout Ontario, with the exception of swampy areas, there are probably few timber stands without their fire history." The quiltwork pattern of stand age-classes in northern Ontario suggests that lethal, stand-replacing, high-intensity surface and/or crown fires are characteristic of the area. Further south the effects of sublethal, low-intensity surface fires are more pronounced. Hence, elucidation of the fire regime requires that the temporal pattern of burning be emphasized--area extent in the former area and return intervals at point locations in the latter.

The purpose of this paper is to explore the scope of our knowledge and ability to reconstruct fire history in Ontario and, finally, to identify the areas where future research efforts will be most fruitful. It is based on a review of published literature and unpublished reports, personal contacts with other workers, familiarization with available written historical sources and five seasons of direct and related field experiences in northern Ontario. This problem analysis is especially timely for someone who has taken on the task of "deciphering the historical nature of wildfire in the Boreal and northern Great Lakes-St. Lawrence Forest Regions of Onatrio." The paper is organized into three recognizable time periods from the standpoint of fire history--modern (since 1920), presettlement (1600-1920), and paleoecological (Holocene deglaciation). Furthermore, the presettlement fire record has been subdivided to cover the following topics: written accounts, tree-ring and fire scar dating, mapping of fire patterns, and stand age-class distribution.

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[3] Heinselman, M.L. 1975. The history and natural role of forest fires in the lower Athabasca Valley, Jasper National Park, Alberta. Unpublished report. 63 p. [Contract Report NOR 5-980-1 on file with Canadian Forestry Service, Northern Forest Research Centre, Edmonton, Alta.].

FOREST ECOSYSTEMS OF ONTARIO

Rowe's (1972) forest regions and sections of Canada have been utilized in this paper partially as a synthesizing framework of available information (fig. 1). Where appropriate, forest section designations have been included. In addition, the latitude and longitude of place names have been included for reader convenience and reference. A forest region is a major geographical belt or zone, characterized vegetationally by a broad uniformity both in physiognomy and in the composition of the dominant tree species. Regional subdivisions, or forest sections, are geographical areas possessing an individuality which is expressed relative to other sections in a distinctive patterning of vegetation and physiography. Rowe (1972) provides a brief description of each forest section.

Three of Canada's eight major forest regions occur in Ontario. The Deciduous Forest Region, restricted to the southwestern part of the province, occurs only in Ontario and is similar to the deciduous forests of the eastern United States. The natural forest vegetation of this region has been largely eliminated by settlement and urbanization. The Great Lakes-St. Lawrence Forest Region of Canada is composed of 16 sections. Three entire forest sections and portions of eight others occur in Ontario. The most outstanding vegetational features of the region are the eastern white pines (*Pinus strobus* L.) and red pines (*P. resinosa* Ait.) although the forests contain a number of other conifers and several deciduous species, resulting in many mixed stands. Much of the area has been influenced by settlement and logging has taken its toll; only portions of the original vegetation remain intact. The vast Boreal Forest Region of Canada is composed of 45 forest sections, of which four entire sections and portions of six others are found in Ontario. The major tree species are jack pine (*P. banksiana* Lamb.), black spruce (*Picea mariana* [Mill.] B.S.P.), white spruce (*P. glauca* [Moench] Voss), balsam fir (*Abies balsamea* [L.] Mill.), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.). Unexploited forests still exist in large blocks. In reality, there is a continuum of various broadleaf deciduous forests in southern Ontario to largely coniferous forests in the north.

There are three major physiographic regions in Ontario (Rowe 1972). The Hudson Bay Lowland (B.5 and B.32) is a poorly drained region abounding in bogs and shallow lakes. The Canadian Shield, comprising the remainder of the boreal forest and most of the Great Lakes-St. Lawrence Forest Region, is characterized by Precambrian bedrock covered with a shallow layer of stony sandy till with knob/ridge topography and an extensive network of streams, rivers, lakes and bogs. Southern Ontario, chiefly D.1, is principally a gently sloping plain.

Worth noting is that mean total annual precipitation, a principal determinant of fire climate, increases on a west to east gradient and decreases from south to north (Brown et al. 1968, Chapman and Thomas 1968). Lightning fire densities in Ontario have recently been mapped for the twelve-year period 1965-1976 (Stocks and Hartley 1979). Lightning fire incidence decreases significantly as one moves eastward. The boreal (excluding B.5 and B.32) and Great Lakes-St. Lawrence forests experience between 0.5 and 3.0 lightning fires per 1,000 km^2 per year (2-12 fires/1,000,000 acres/yr).

MODERN FIRE RECORD

Formal fire reporting by the provincial forestry service (now Ontario Ministry of Natural Resources) began in 1917 and by the 1920s most of Ontario north to approximately latitude 52° was being consistently covered. Data on B.32 and the northern portions of sections B.5 and B.22a prior to 1970 are incomplete. The first attempt to summarize the areal extent of forest fires from these reports was the inclusion of Map No. 9 (Reported Burned Areas of over 500 Acres) in the report of the 1947 Ontario Royal Commission on Forestry (Anonymous 1947b). Fire areas were color coded by two time periods (1920-1935 and 1936-1946) on a single map sheet at a scale of 1 inch to 50 miles (1 cm ≈ 31.7 km). Donnelly and Harrington (1978) have since produced an "atlas" comprising seven maps at a scale of 1:500,000 for all fires 200 hectares (500 acres) and larger covering the period 1920-1976. Individual fires have been identified by year and Rowe's (1972) forest section boundaries have been included as well. It is thought that about 95 percent of the total area burned is represented by these fires. Harrington and Donnelly (1978) subsequently compiled area burned data and computed the percentage of area burned annually by decade for several sections in northern Ontario. Their work has been updated only slightly in this paper by including fire report information for the period 1977-1979. On the basis of the average annual rate of burning, over the relatively short period during which records have been kept (i.e., the past 60 years), the present fire cycle for northern Ontario is calculated to be approximately 500 years (table 1), and this presumably reflects increasing fire control effectiveness.

PRESETTLEMENT FIRE RECORD

Written Accounts

Two of the best known historic fires in Ontario prior to 1920 are unfortunately associated with human disaster. An estimated 73 persons lost

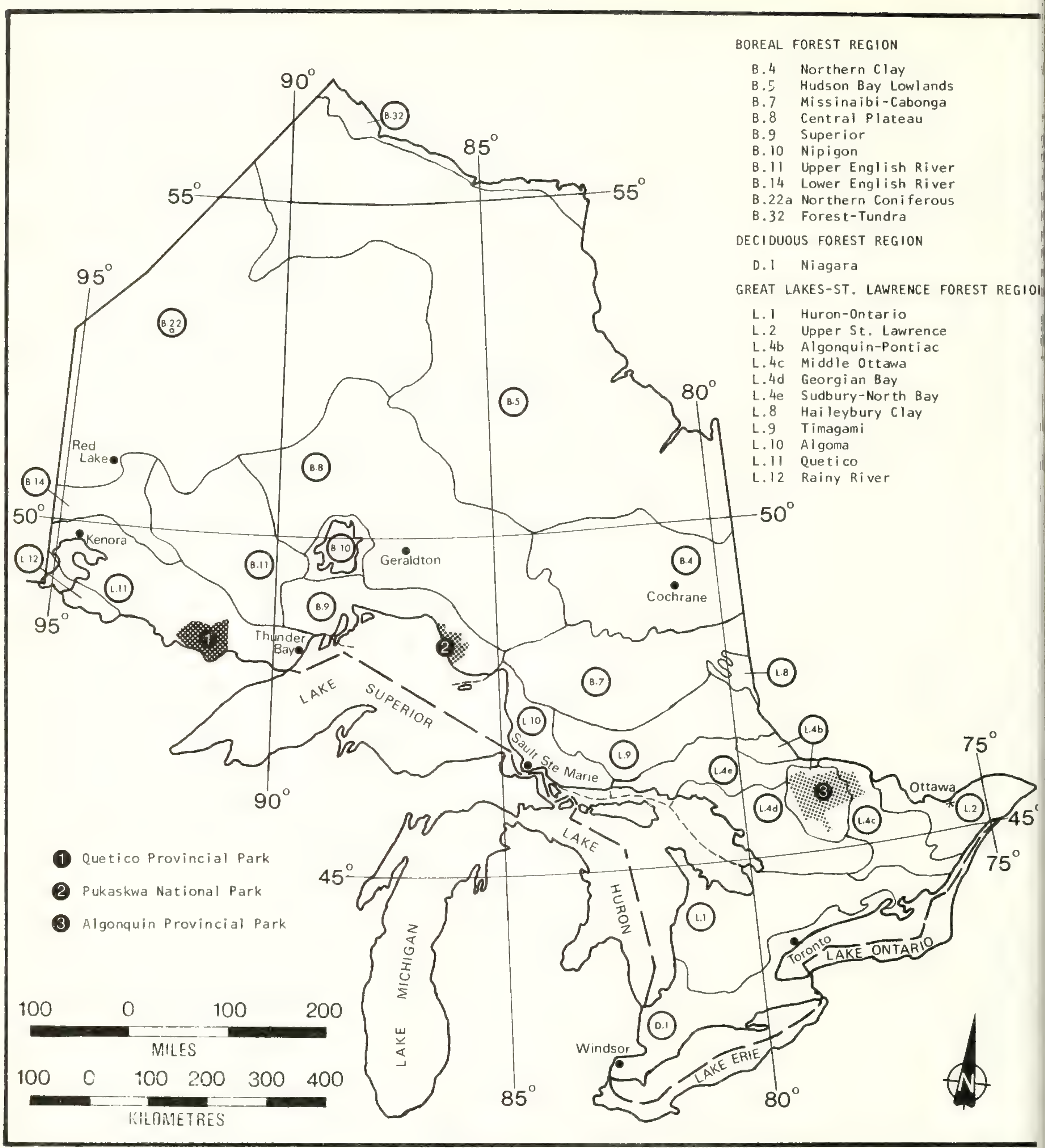

Figure 1.-- Map of forest regions and sections in Ontario according to Rowe (1972).

ole 1.--Percentage of area burned annually (by decade) and calculated fire cycle for selected geographical regions in northern Ontario based on all fires greater than 200 ha (500 acres) in size that were reported between 1920 and 1979 (adapted from Harrington and Donnelly 1978; includes data for period 1977-79).

orest Region and Section (after Rowe 1972)	Size of Area (acres[1])	% Mean Annual Burned Area[2]							Fire Cycle[3] (yr)
		1920-29	1930-39	1940-49	1950-59	1960-69	1970-79	1920-79	
real	82,319,220	0.30	0.28	0.14	0.07	0.15	0.20	0.19	526
rthern Clay (B.4)	13,327,909	.17	.03	.05	.08	.0	.03	.06	1,667
ssinaibi-Cabonga (B.7)	10,763,952	.44	.16	.49	.19	.02	.02	.22	455
ntral Plateau (B.8)[4]	24,881,238	.42	.19	.03	.05	.03	.15	.15	667
perior (B.19)	5,852,452	.08	.88	.25	.02	.0	.01	.21	476
pigon (B.10)	1,200,965	.17	.02	.27	.69	.0	.0	.19	526
per English River (B.11)	10,189,529	.19	.46	.08	.0	.12	.13	.16	625
wer English River (B.14)	3,555,317	.58	.16	.05	.05	.04	.02	.15	667
rthern Coniferous (B.22a)[4]	12,547,857	.23	.46	.16	.03	.81	.86	.43	233
eat Lakes-St. Lawrence									
etico (L.11)	10,757,111	.51	.60	.03	.01	.01	.14	.22	455

[1] Acres x 0.4047 = hectares.

[2] The percentages were computed under the assumption that the portion of the surface covered by water within e boundaries of the burned areas was equal to that in the region at large (Harrington and Donnelly 1978).

[3] Based on the average rate of burning for the period 1920-1979. The reciprocal of the calculated fire cycle the proportion of the whole region that burned annually (Van Wagner 1978).

[4] Includes that area south of latitude 52°N within the section.

their lives in a fire covering 864 mi^2 (2,238 km^2) in the newly opened mining country between Porcupine (48°30'N, 81°10'W) and Cochrane (49°4'N, 81°01'W) in 1911. In 1916, 224 people perished in a fire that covered more than 1,000 mi^2 (2,590 km^2) centered around the community of Matheson (48°32'N, 80°28'W). Numerous accounts of forest fires prior to the initiation of province-wide reporting can be found in several printed sources. The detail varies considerably, from general observations of causes and major fire years in certain locales to specific information on location and approximate areal extent of individual fires. Only a few examples can be given here to illustrate the wealth and value of fire history information available in published and unpublished forms.

Some of the earliest written accounts of forest fires were by Jesuit priests serving at various missions throughout eastern North America. Father Jean Pierre Aulneau remakred that the smoke from forest fires was so thick that it prevented him from "even once catching a glimpse of the sun" as he travelled from Lake Superior to Fort St. Charles (Minnesota) on Lake of the Woods (49°18'N, 94°52'W) in 1735 (Nute 1950). Many of the Jesuit writings are recorded in several published volumes (Thwaites 1901). However, as Leslie[4] rightly notes, "...it is difficult to tie these records to an actual area."

The chronicles of the first Europeans to traverse the country also served to document fire incidence. Alexander MacKenzie, a renowned explorer of northern Canada, mentioned that large fires occurred north of Lake Superior in 1788 and 1789 (Leslie[4]). Many diaries have been published and a considerable amount of unpublished material can be found in the Archives of Ontario in Toronto and the Public Archives of Canada in Ottawa.

Records associated with the fur trading companies contain entries of forest fires near established posts and in surrounding areas. An excellent map showing post locations and approximate length of operation is available (Anonymous 1973). The journals and reports of the Hudson's Bay Company (HBC) post traders are particularly useful and as Leslie[4] suggests "...would repay further study." J.D. Cameron, the HBC trader at Rainy Lake (48°50'N, 93°05'W), wrote that 1803 and 1804 were major fire years along the Minnesota/Ontario lakeland border country (Nute 1941, 1950). Charles McKenzie, the HBC trader at Osnaburgh House (51°08'N, 90°16'W), noted that a large part of the country between the post and the Winnipeg River in southern Manitoba was burned over in 1825 (Bishop 1974). The original HBC records are located in the Company's archives in Winnipeg, Manitoba. Microfilm copies have been filed with the Public Archives of Canada.

The field notes and maps of the Ontario provincial land surveyors (PLS) constitute an invaluable record of forest fire history (Weaver 1968). An excellent example is the published account of an extensive exploratory survey of some 60 million acres (24 million ha) in northern Ontario during 1900 (Anonymous 1901). The area was divided into ten districts and one field party was detailed to examine each district. Meridian and base line surveys which passed through miles of country afforded the opportunity to tie observations of forest fires to specific locations with a high degree of accuracy (Richardson 1929, Leslie[4]). For example, extensive portions of the country north and west of Lake Superior and as far west as Rainy Lake (48°42'N, 93°10'W) are known to have been burned over in 1845. The eastern parts of Algonquin Provincial Park were swept by fire in 1851. fires in 1855 covered an estimated 2,000 mi^2 (5,180 km^2) between the west shore of Lake Timiskaming (46°52'N, 79°15'W) and Michipicotn (47°57'N, 84°54'W) on Lake Superior. In 1864, two separate fires joined, finally covering a distance of approximately 170 miles (275 km) from the Thessalon River (46°15'N, 83°34'W) on Lake Huron to Lake Nipissing (46°17'N, 80°00'W). Fires covered more than 2,000 mi^2 (5,180 km^2) north of Lake Huron in 1871 from Lake Nipissing to the Mississagi River (46°34'N, 83°22'W). Township surveys are a very specific source of data on past fire occurrence. For example, PLS Hugh Wilson laid out the 63,630 acre (25,751 ha) Pic Township (48°41"N, 86°17'W) on Lake Superior in 1873 and determined that a large portion had been overrun by fire in 1869 (Kirkwood and Murphy 1878). Ontario is nearly covered by townships north to approximately latitude 50° and west to longitude 85° (Weaver 1968). In the remainder of the province, townships are clustered around existing population centers. The unpublished documents and maps associated with the various PLS surveys are on file with the Surveys and Mapping Branch of the Ontario Ministry of Natural Resources in Toronto.

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[4] Leslie, A.P. 1954. Large forest fires in Ontario. Unpublished report. Ontario Department of Lands and Forests, Toronto. 16 p. [copy on file with Aviation and Fire Management Centre, Ontario Ministry of Natural Resources, Sault Ste. Marie].

References to forest fires are also found in the published reports and maps of the Ontario Bureau of Mines and Geological Survey of Canada (e.g., Ferrier 1920, Nicolas 1921). For instance, during his travels in 1888 through the Hunter's Island area in what is now Quetico Provincial Park, Smith (1892) stated that there had been three recent periods of fire: in 1870, 1879 and 1885-1886. He gives a long list of lakes whose shores showed evidence of those fire episodes. Bell (1904) describes an area of over 3,000 mi^2 (7,770 km^2) that burned in 1901 south and west of Lake Kesagami (50°23'N, 80°15'W). Collins (1909) remarked that much of the country between the east and west branches of the Montreal River (47°08'N, 79°27'W) was swept by several fires in September, 1908.

The relative roles of lightning and man as ignition sources during the presettlement era are known only qualitatively. As Wright and Heinselman (1973) point out, though, "The key question is whether lightning alone is an adequate source of ignition to account for the observed extent of burning in given ecosystems." Lutz (1959), in his review of the various historical causes of fire in the boreal forest, was of the opinion that lightning was certainly responsible for starting fires but that man had been a more important cause. There is little doubt that man has been a factor in the proportion of area burned (Richardson 1929, Sharpe and Brodie 1931, Leslie[4] particularly through his carelessness with campfires. The white man's intentional use of fire in those activities associated with prospecting and the railroad in the late 1800s and early 1900s is a case in point. For example, there were two large fires in 1891 and 1896 along the Canadian Pacific Railroad line (Richardson 1929) between Pogamasing (46°55'N, 81°46'W) and Woman River (47°31'N, 82°38'W), a distance of some 80 miles (129 km).

The extent to which natives used "prescribed" fire in their culture is difficult to assess. Harnden[5] related an interesting account of the use of fire by Indians for wildlife habitat improvement. In 1948, during a canoe trip on Poshokagan Lake (49°22'N, 90°20'W), 80 miles northwest of Thunder Bay, he met a French immigrant who had lived most of his life with the native Indians of northwestern Ontario. At the time, the man was approximately 75 years of age, having arrived in northwestern Ontario when he was about 17. The Indians were apparently well aware that young vigorous forests were usually the most suitable habitat for a large variety of animal and plant species. In order to maintain sufficient areas suitable to their needs, Indian bands set fire to selected areas at appropriate times and thus manipulated the forests. Consequently, over the long term, perhaps a generation or more, most of northwestern Ontario was burned by the Indians.

Assessing the influence of man-caused fires on the regime may be immaterial, for man probably served merely as an alternative ignition source in most areas. Fuels and weather determined whether ecologically significant fires occurred (Heinselman 1973). Any detrimental effects associated with a short-interval fire regime were probably localized and in most cases not of great significance on a regional scale except for those situations where repeated fires followed logging and land clearing (Howe 1915, Sharpe and Brodie 1931).

Tree-Ring And Fire Scar Dating

Some 50 years ago Richardson (1929) in his booklet on Ontario forestry wrote "...strange as it may seem, the magnificent pineries composed as they were of trees nearly all of the same age, were the result of forest fires which occurred some time in the distant past." Richardson was undoubtedly referring to red and white pine stands which are reasonably reliable as a source of fire dates, but there is a period between the time fire occurs and the time natural regeneration begins, and this period must be taken into account when one tries to determine exact fire dates. Jack pine, and to some extent black spruce, are especially good colonizers following fire. Ring counts of aspen and birch are especially difficult. White spruce can be used to obtain "minimum" fire origin dates.

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[5] Harnden, A.A. 1978. Personal correspondence. Canadian Forestry Service, Great Lakes Forest Research Centre, Sault Ste. Marie, Ont.

Red and white pine each have a maximum lifespan of 400 years, although the latter is more prone to decay. White and black spruce may live for up to 250-300 years, but for the latter such ages are encountered only in rather large lowland areas. Jack pine stands seldom exceed 200 years. The preceding estimates are based on values found in the literature for Ontario and on personal experience. For instance, one of the oldest known intact jack pine stands in Ontario (*ca.* 1772 fire origin) is found along the Aubinadong River (46°52'N, 82°24'W; L.9). No standard correction factors for increment boring height (in order to arrive at total age) are available although these could be developed from stem analysis data available for large trees, by progressive measurement of seedling heights on recent wildfire sites, and/or by aging seedlings. Factors no doubt vary according to site conditions.

Jack and red pine constitute the most abundant source of live basal fire scar material in the north and south, respectively. Double fire scars are reasonably common on jack pine (fig. 2). For example, we were able to document the origin, 1899, and previous fires, 1831 and *ca.* 1780 (corrected pith year), for an experimental fire study area in a mature jack pine stand near Kenshoe Lake (48°56'N, 85°16'W; B.8). Triple scars are exceedingly uncommon. In only one case during a survey of over a hundred fire origin stands in northwestern Ontario was a triple encountered. Approximately 12.5 miles (20 km) northeast of the town of Pickle Lake (51°35'N, 90°00'; B.22a) a triple fire scar cross-section collected in 1978 revealed fires in 1929, 1863, 1835 and *ca.* 1799 (corrected pith year). Red pine has a great resistance to decay resulting from fire scars, as is readily apparent in a cross-section taken in 1980 from a specimen (*ca.* 1671 origin) on Kwinkwaga Lake (48°49'N, 85°20'W; B.8) exhibiting evidence of fires in 1829 and 1818.

Dead fire scar material has been found to be an invaluable means of extending fire chronologies back in time. As part of the survey referred to earlier, a double fire-scarred jack pine killed in a known fire (1932) area on Tackaberry Lake (51°23'N, 93°05'W; B.22a) was collected in 1976 and showed evidence of fires in 1845, 1807 and *ca.* 1792 (corrected pith year). Fire scars on recent wildfire sites have proven useful in documenting stand history associated with permanent regeneration plots on these areas. Near the Allan Water train stop on the Canadian Pacific Railroad line (50°14'N, 90°12'W; B.11) a 1976 fire-killed jack pine revealed previous fires on the site in 1910, 1843, and *ca.* 1797 (corrected pith year).

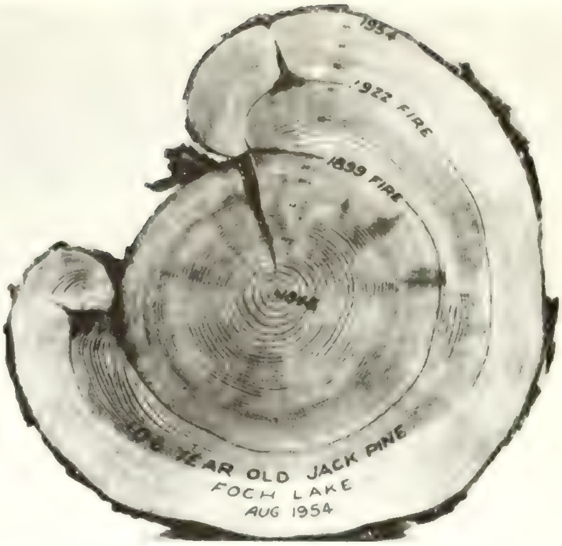

Figure 2.--Cross-section of a double fire-scarred jack pine collected near Foch Lake (49°15'N, 85°20'W; B.8) in August, 1954 for stand aging purposes during a timber cruising operation. The second scar date was inadvertently mislabelled 1922 instead of 1923. The spceimen measures 10 inches (25 cm) in width. (Photo courtesy of The Ontario Paper Company Limited, Manitouwadge, Ont.).

Rondeau Provincial Park, located on the north shore of Lake Erie (42°17'N, 81°51'W; D.1), is a 4,450 acre (1800 ha) remnant of the deciduous forest that once covered most of the southwestern peninsula of Ontario before the days of the early settlers. Bartlett (1956) obtained the ages of 610 trees from increment cores at DBH and freshly cut stumps during an extensive examination of age-class composition in 1954. Sixty saplings were subjected to stem analysis and average correction factors were computed in order to arrive at total age (6 yr for DBH height and 2 yr for stump height). Bartlett concluded that fires were "common" in the white pine-oak (*Quercus* sp.) forest type between 1664 and 1839. The oldest, even-aged groups of white pine were regarded as having originated following fire between *ca.* 1749 and 1758. The broad distribution of ages obtained in the hardwood forest type suggested that the community had been relatively undisturbed by fires since at least 1664. Heinselman[6] was forced to rely almost soley on increment cores from white spruce in estimating fire origin dates for the Slate Islands located along the north shore of Lake Superior (48°40'N, 87°00'W; B.9). During a brief 3-day field trip he was able to reconstruct a major portion of the area's fire history which was required for an evaluation of woodland caribou habitat characteristics.

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[6] Heinselman, M.L. 1978. Personal conversation. Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minn.

The stand (fire) origin of a 367-acre (149 ha) silvicultural experimental study area (49°00'N, 85°49'W; B.8) southeast of Manitouwadge was determined as *ca.* 1761 (Hughes 1967). A careful search for fire scars in the upland mixedwood stand failed to reveal any fire scars except for a small segment that burned in 1850 and a 1922 fire that passed nearby.

Turner (1950) reconstructed the fire history for several of his spruce budworm-forest impact study areas using tee-ring counts and basal fire scars. For example, in the Mississagi River area (47°00'N, 83°00'W; L.9) he found in 1946 that the ages of most white, red and jack pine stands were all between 160 and 165 years. This corresponds to Sharpe and Brodie's (1931) observation that "In parts of the Mississagi Provincial Forest white pine was found to be in the neighbourhood of 350 years of age and carrying two fire scars, one about 150 years ago [1780] and the first one about 250 years ago [1680]." At his Manitowik Lake-Michipoten River location (48°00'N, 84°30'W; B.7) he found scar evidence for fires in 1790, 1828, 1845, 1875, 1878, 1891 and 1901.

Howe (1915) undertook a detailed survey of forest conditions in areas that had burned once, twice, three and several times within Methuen Township, and a portion of Burleigh Township (44°40'N, 78°03'W; L.1). The total area involved amounted to 86,333 acres (34,939 ha). From tree-ring counts of aspen and fire scar dating of red and white pine he documented fires in 1880, 1890, 1895, 1897, 1899, 1905, 1907 and 1910. (I am assuming that "years" date from a reference year of 1915). A cross-section from a single fire-scarred red pine snag disclosed that it has been scarred when it was 25, 43, 55, 64, 82, 88, 96 and 100 years old. This corresponds to a return interval of 12.5 years. The photo of a *ca.* 1678 origin triple fire-scarred red pine cross-section showing fires in 1744, 1756, and 1766 from his report was reprinted in a short popularized article (Anonymous 1923).

Bickerstaff (1942) reported that much of the Petawawa Forest Experiment Station (now Petawawa National Forestry Institute) which shares Algonquin Park's northeast boundary (46°00'N, 72°26'W; L.4c) has been repeatedly swept by fire since at least 1647, with dated fires occurring in 1716, 1748, 1832, 1862 and 1875. Six major fires were reported to have occurred between 1860 and 1919 (Anonymous 1947a). Brace (1972) found fire scar evidence for fires prior to 1920 in 1854, 1871, and 1892. From written and forest records Burgess (1976) was able to document eight separate fire events during the last 300 years for a mixed jack-red-white pine area on the Station. The average fire interval over this time was approximately 37 years (Burgess and Methven 1977).

A red pine fire-scarred cross-section taken from a mixed pine stand in the Parke Township (46°30'N, 84°30'W; L.10) near Sault Ste. Marie revealed an average return interval of 30 years with a range of 14-46 years on the basis of five fire events for the period 1727-1877 (Alexander et al. 1979). The cross-section and entire "cat face" have been developed into a display located in the Great Lakes Forest Research Centre's (GLFRC) main entrance area. Approximately 900 people visit the Centre during the summer months. Further fire scar and tre-ring dating in the 5,300-acre (2,145 ha) township was completed in 1979 and 1980. This work is being done by Stephen W.J. Dominy, a forestry student at Lakehead University in Thunder Bay who is supported in part by GLFRC. The results form the basis of a Bachelor of Science thesis due to be completed in May 1981.

Cwynar (1975, 1977) developed a presettlement fire chronolgy, principally from wedges of red pine fire scars, for the 45,960-acre (18,600 ha) Barron Township which lies in the east half of Algonquin Provincial Park (45°53'N, 77°54'W; L.4b). Sampling was carried out by foot and canoe during the summer of 1974. Sixteen fire years were identified as having occurred between 1696 and 1920. Accuracy of the fire scar dating was judged to be ± 2 or 3 years. Increment cores were also taken from dominant trees at most fire scar sites.

Woods and Day (1976, 1977) reconstructed the presettlement fire history of a 230,000 acre (93,080 ha) portion of Quetico Provincial Park, known as Hunter Island, by aging wedges of basal fire scars and increment cores of fire-initiated stand age-classes. Because of possible inaccuracies in age determinations, fire origin dates were placed in 10-year periods going back to 1770. The sampling was carried out during the 1975 and 1976 field seasons and was confined to areas along major waterways which afforded access by canoe.

A current study in the 460,000-acre (186,000 ha) Pukaskwa National Park involves the use of increment cores from fire-initiated stands and basal fire scar cross-sections of live residuals and snags to construct a chronology of major fire years (Alexander 1978). Access and the shear size of the area posed a formidable challenge. The shoreline area and adjacent islands in Lake Superior were intensively sampled by motorboat. Over 125 sample sites were selectively located in the interior of the park on the basis of a careful review of existing forest inventory maps. Most of these areas were reached with a Hughes 500D helicopter. Sampling was carried out during portions of the 1977-79 field seasons. The field data are being supplemented by stand aging information collected as part of a biophysical resource inventory of the park. Where possible, fire origin dates are bieng confirmed by written accounts. The climatic history of the park and its relation to fire occurrence are also being investigated in a cooperative study with dendroclimatologists M.L. Parker and L.A. Jozsa of the Forintek Canada Corp.'s Western Forest Products Laboratory n Vancouver, British Columbia. Red pine (the astern cousin of ponderosa pine) stands were ampled at four locations and the increment cores ere subjected to X-ray densitometry techniques. nalysis and interpretation of the data are still n progress.

Mapping Fire Patterns

Fry[7] notes that "...an age-class distribution ap for a management unit in northern Ontario is ittle more than a mosaic that visually tells us here fires burned, when they burned and what they ooked like in terms of area covered." Recent urns were mapped (chiefly by aerial sketching) uring province-wide forest surveys in the 1920s (Sharpe and Brodie 1931). This represents the arliest mapping of fire patterns at such a large cale with reasonably accurate detail. Reconstructing historic fire patterns is no doubt more readily ccomplished in northern Ontario than further south.

Howe (1915) was able to produce a "fire incidence" map for Methuen and Burleigh Townships at a scale of 1 inch to 2 miles (1 cm ≈ 1.27 km) from the fire scar and tree-ring data gathered along cruise lines. Recent burn areas comprised 51,334 acres (20,775 ha) of the total 84,333 acres (34,130 ha) of forested area under investigation. Areas burned once, twice, three and many times (since the present stand establishment) comprised 33.8, 34.6, 13.6, and 18.0 percent of the study area, respectively. Cwynar (1975, 1977) was not able to develop true fire history or stand origin maps (Heinselman 1973). Instead he reproduced maps in which fire scar locations and fire-initiated forest stands, presented separately, were used to show the approximate areal extent of eight major fire years between 1763 and 1914, five of which covered more than half the township (1763, 1780, 1854, 1864, 1875).

Lynn and Zoltai (1965) developed a stand origin map at a scale of 0.75 inch to 1 mile (1 cm ≈ 1.18 km) for a 21.0 mi^2 (54.4 km^2) area (49°56'N, 87°07'W; B.8) northwest of Geraldton from forest inventory maps and stand aging data. An area of approximately 12 mi^2 (31 km^2) was delineated as having burned in 1880. An area of about 5 mi^2 (13 km^2) was swept by fire in 1920, 1922 and 1923 while the remaining area was burned in 1830, 1852, 1860, and 1870.

Woods and Day (1976) initially produced a "burn period" map at a scale of 1 inch to 1 mile (1 cm ≈ 1.58 km) for approximately 100,000 acres (40,500 ha) of their Hunter Island study are from data collected in 1975, existing forest inventory maps, and interpretation of 1948 and 1965 aerial photos. This was subsequently combined with further information collected in 1976 and with photo interpretation, and a final map was printed at a scale of 2 inches to 2.65 miles (1 cm ≈ 1.19 km) with areas delineated by decade intervals back to 1770 (Woods and Day 1977). Over 75 percent of the study area was burned over between 1860 and 1919.

Stand origin and fire history maps for Pukaskwa National Park are being produced from the tree-ring/fire scar data tied to forest inventory maps from stereoscopially interpreted aerial photographs taken in 1949, 1963, and 1973. The northern half of the park also has 1937 photo coverage. The 1949 maps constitute the most compelte and reliable inforamtion on forest stand mosaics. Stands were delineated by 20-year age-class groups up to 140+ yr. The entire project was supervised by S.T.B. Losee, a pioneer of forest aerial photo interpretation in eastern Canada. Extrapolations of field data to adjacent areas are being made out of necessity.

Harrington[8] has illustrated the potential of satellite imagery in mapping fire patterns for a pilot study area near Trout Lake in northwestern Ontario (51°12'N, 93°07'; B.22a) that has a history of large fires between 1932 and 1976. Recent fire mosaics were readily identifiable and appeared as bright to progressively darker colors. Older age-classes (1915 and 1856) were very dark blue. Remote sensing is a rapidly advancing technology in northern Canada. It will very likely paly a major role in future fire history investigations.

Stand Age-Class Distribution

Brodie and Sharpe (1931), in their publication on Ontario's forest resources stated that "...fires have occurred periodically up to the present time, giving rise to series of age-classes, thus providing an opportunity for seeing the development of stands from youth to maturity." Germane to this section of the paper are some additional statements and observations from various surveys conducted in northern Ontario during the 1950s and 1960s. MacLean and Bedell (1955) noted that most parts of the Northern Clay belt (B.4) had:

> ...burned at least once during the past 130 or 140 years, and even-aged stands predominate The age-class distribution indicates that widespread fires took place about 1820, between 1850 and 1865, about 1895, and in 1923. It appears that dry condi-

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[7] Fry, R.D. 1976. Prescribed fire in the forest. Paper presented at the Ontario Ministry of Natural Resources Prescribed Burning Seminars (November 23-25, Quetico Centre and November 30 - December 2, L.M. Frost Natural Resources Centre). 22 p.

[8] Harrington, J.B. 1976. LANDSAT imagery applied to the ecology of the Canadian boreal forest. Paper presented at the Fourth National Conference on Fire and Forest Meteorology (St. Louis, Missouri, November 16-18). 4 p.

> tions accompanied by high fire frequency, occur at about 30-year intervals. This conclusion is substantiated by similar findings to the south and east in Forest Section B.7. Owing to the flat nature of the topography, the fires burned over the whole landscape, from the driest sand plains to the wettest swamps. In this respect Forest Section B.4 differs from Forest Section B.9 where the topogrpahy is much rougher, fires are usually confined to the higher ground, and great difficulty is encountered in finding swamps which have been burned in the past 120 years...[Bedell and MacLean 1952 were not able to find any stands > 200 years in more than 600 examined in B.9].

MacLean (1960) stated that most mixedwood stands in sections B.4, B.8, and B.9 had:

> ...originated from fires which took place since the year 1800. Stands from earlier fires are infrequent and rarely extensive. However, a few of these very old stands were found in each of three sections under consideration.

Zoltai (1965) made the following comment about northwestern Ontario (principally sections L.11, B.11 and B.14):

> The fire disturbance is so widespread throughout the region that areas not burned within the last 100-150 years are exceedingly rare.

These statements indicate that the frequency or distribution of stand age-class is a major feature of northern Ontario's forest landscape strongly associated with the area's fire history and that differences in the geographical pattern of burning do exist.

Heinselman (1973) referred to the average time required for fire to burn over an area equivalent to the total area under consideration prior to fire suppression as the natural fire rotation. Van Wagner (1978) used the term fire cycle to mean the same thing. The definition is worded in this way to allow for the likelihood that some portions of the area will experience shorter return intervals while others will be missed by fire for fairly long periods. The fire rotation or cycle is the appropriate yardstick of forest renewal in natural fire-dependent ecosystems. Cwynar (1975, 1977) deduced a presettlement fire rotation of 70 years for Barron Township on the basis of the conservative assumption that fires during the five major fire years covered at least half of the area and tha small fires in 1844, 1889, and 1914 each burned a quarter of the township. Wodds and Day (1977) calculated a natural fire rotation, founded on the best period of record prior to 1920 (i.e., 1860-1919), of 78 years. An inherent problem in using a percent annual burn figure derived from reconstructed fire year maps in calculating fire rotations or cycles is the loss of record of the exact area burned by past fires because of succeeding fire events.

Van Wagner (1978) has illustrated that the distribution of stand age-classes in natural fire-dependent forest ecosystems experiencing a stand renewing fire regime should, if we assume a random ignition pattern and uniform flammability regardless of age, match a negative exponential (NX) function. The assumptions used in the model require clarification. Lightning fire ignitions occur in a more or less random fashion and any non-uniformity in flammability throughout the fire cycle is not likely to affect the age-class distribution (ACD) adversely. The NX model of ACD predicts that about one-third of the forest is older and that two-thirds is younger than the fire cycle which is equal to the mean stand age. The average interval between fires at a given point is theoretically the same quantity as the fire cycle. Van Wagner (1978) has shown that Heinselman's (1973) stand origin map data for the remaining 415,000 acres (168,000 ha) of virgin forest in the Boundary Waters Canoe Area, which borders Quetico Provincial Park on the north, to fit a NX distribution approximating a presettlement fire cycle of 50 years. This differs considerably from the natural fire rotation of 100 years derived earlier by Heinselman (1973) for his entire 1,000,000 acre (404,700 ha) study area. Van Wagner's (1978) concept of fire cycle is also appropriate to a particular forest vetetation type that is intermingled on a regional scale with other types that have different cycles. Upland forest types no doubt have variable fire cycles and are certainly shorter than those for lowland communities.

The NX model of ACD can be used to determine fire cycles for forests such as those found in northern Ontario. Its main advantage over other model forms is its simplicity.[9] The mathematics is easy, the resulting graphic model is easily visualized, and a less than perfect fit may be interpreted as mere roughness in the natural fire process. One might suspect that fire cycles could be estimated from stand data generated by Ontario's forest inventory program (Anonymous 1978) but it is doubtful that the classification of stand age groups delineated almost wholly from interpretation of aerial photographs is sufficiently precise to permit accurate determinations. Calculations must therefore depend on the distribution of stand ages obtained by random sampling. A large body of data is needed, both on the area sampled and on the age of stands, to obtain a good statistical fit.[9] A forest section might be regarded as a sufficiently large area. An alternative to sampling would be stand origin map data such as Heinselman's (1973). The old age tail is an important aspect of the NX model and must be carefully accounted for in the study area.[9]

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[9] Van Wagner, C.E. 1980. Personal correspondence. Canadian Forestry Service, Petawawa National Forestry Institute, Chalk River, Ont.

Some mention should be made here of computer modelling of stand age-class distributions and related interactions. The simulations of ACD influenced by random fire and timber harvesting such as those presented by Van Wagner (1978) can provide considerable information that will be useful in planning fire and land management strategies. A further example of fire history-ecology modelling is offered by Suffling et al. (1980) who developed scenarios for projections in stand ACD, species composition and furbearer population changes over time, until the year 2017, as influenced by fire control, fire control and logging, and a completely natural regime of fire and no logging.

PALEOECOLOGICAL FIRE RECORD

The oldest positive evidence of fire in Ontario comes from charred wood remains, found 200-300 feet (60-90 m) below the surface at Scarborough Heights near Toronto (Penhallow 1904), which dated back to the Early Wisconsin glacial period (60,000-70,000 years ago). Terasmae (1967) attributed the consistently high percentages of jack pine and white birch pollen found in core sediments from Nungesser Lake in northwestern Ontario (51°28'N, 93° 30'W; B.22a) to frequent forest fires in the region throughout postglacial (Holocene) time--more than 9,000 years. Charcoal fragments/depsoits have also been casually noted in core samples of lake and peat bog sediments taken for palynological studies. For example, "charcoal bookmarks" at varying depths, dating back to deglaciation (8,000-11,000 years ago) have been documented at Harrowsmith Bog (44°25'N, 76°42'W; L.1) in southern Ontario (Terasmae 1969) and in Thane Lake (48°20'N, 84° 59'W; B.8) in northern Ontario (Terasmae 1967).

The only charcoal stratigraphy studies of lake sediments (combined with pollen analysis) undertaken in Ontario are confined to Algonquin Provincial Park and nearby areas. Cwynar (1975, 1978) analyzed a 500-year section of laminated sediment for charcoal influx from Greenleaf Lake (46°63'N, 77°57'W; L.4c) on the east side of the Park. Six distinct peaks documented between 770 and 1270 A.D. resulted in a fire return interval of approximately 80 years for the lake's drainage basin. Terasmae and Weeks (1979) examined the extent of charcoal abundance and frequency of occurrence at Found Lake (45°31'N, 78°31'W; L.4b) in the southwestern portion of the park, and at Perch Lake (46°02'N, 72°21'W; L.4c) and Boulter Lake (46°09'N, 79°02'W; L.4b) east and northwest of the park, respectively. An additional site, Lac Louis (47°15'N, 79°07'W), approximately 16 miles (26 km) east of the Ontario/Quebec border and within section B.8, was also sampled. The Found Lake sediment revealed a sparseness of charcoal whereas the limited core sample from Boulter Lake exhibited both a high frequency and an abundance of charcoal. For Perch Lake, the fire frequency was judged to be 140-150 years. The mean fire frequency in the Lac Louis area was calculated to be 95-100 years for the past 9,000 years but increased to 48-56 years approximately 4,000-7,000 years ago. In support of this work (1976) developed a slide preparation technique for determining the presence of charcoal particles that could be used for continuous sampling of lake sediment cores. All the data reported in Terasmae and Weeks (1979) can be found in Weeks' (1976) undergraduate thesis.

Site selection remains a major consideration in charcoal stratigraphy studies. Meromictic lakes (overturning does not extend to the bottom) are preferred sample locations, but they are exceedingly rare. The Experimental Lakes Area in northwestern Ontario (49°30'-45'N, 93°30'-94°00'W) is known to contain a number of meromictic lakes (Schindler 1971). Schindler[10] has indicated that probably less than one percent of the lakes on the Canadian Precambrian Shield are meromicitc in nature. The exact mechanisms of charcoal dispersal from source to deposition in lakes requires further investigation.

CONCLUSIONS AND RESEARCH NEEDS

Area burned maps on a provincewide scale have been prepared from fire report information for the period since approximately 1920. Fire cycles for the recent past, based on percent annual burn, have been calculated. Written accounts are a potentially useful data source on fire incidence between *ca.* 1700 and 1920. Tree-ring and fire scar dating has been widely used. Reconstructing fire patterns for presettlement times is limited to a few study areas. The mosaic of even-aged forest stands in northern Ontario lends itself well to mathematical deduction and modelling of natural fire cycles. Extension of fire history back to the end of pleistocene glaciation has been at least partially successful but is confined to a small number of concentrated sites.

A question that must be addressed here is: "How much do we need to know about the historical role of fire?" Management concerns and contributions to ecological knowledge must be considered jointly. Fire history information may also have site specific and area specific uses, e.g., for fuel complex assessment, ecological surveys and investigations, insect and disease susceptibility, wildlife habitat evaluation, research study area description, and natural history interpretation. Man has so greatly altered the natural fire regimes of southern Ontario that elucidation would be virtually impossible if not academic in many areas. From a fire and land management perspective, the needs in northern Ontario are great and the information currently available is limited. The complexity of the area coupled with its vastness dictates the neef for a comprehensive study of a single forest section initially. The following research needs represent a compromise between these two interest groups. They should be the focus of a forest fire history research program in Ontario over a 2-to-5-year period. In selecting these research needs I have considered the likelihood of problem solution, the applicability of research results, available resources, and financial limitations.

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[10] Schindler, D.W. 1980. Personal conversation. Department of Fisheries and Ocenas, Western Region, Freshwater Institute, Winnipeg, Man.

1. The written accounts of fire history should be systematically assembled and catalogued, carefully synthesized, and made readily available in the form of a single published compendium or a series of publications. Cooperation with historical geographers would be beneficial.

2. A handbook similar to Arno and Sneck's (1977) should be developed for forest situations found in the boreal and Great Lakes-St. Lawrence regions of Ontario. It should be based on previous local experience and written to cover the perceived uses of fire history information.

3. The Northern Coniferous forest section (B.22a) is a likely candidate area for an integrated study of fire hisotry. It is largely unmodified by logging and fire protection although expansion of these activities is imminent. Fire periodicity is extraordinarily high and so it should serve as a reference by which to gauge the fire regimes of other forest sections. Such a study should involve an integrated team of scientists and consist of random age-class/fire scar sampling, stand origin mapping at representative locations, and charcoal/pollen analysis of selected lakes and bogs. Forest section B.22a is sufficiently large for the application and further testing of Van Wagner's (1978) NX model. Charcoal fragments are known to be rather abundant in post-glacial lake and peat sediments in the area.[11]

4. The relationship between past climatic characteristics and fire history utilizing dendroclimatological techniques needs further investigation but such work should await the results of the pilot effort in Pukaskwa National Park. If red pine tree rings are indeed a sufficiently sensitive barometer of climatic fluctuations then a network of sample sites would be necessary. A number of small red pine stands are found across northern Ontario (Haddow 1948); the northernmost stand is located at Nungesser Lake.

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Fire Recurrence and Vegetation in the Lichen Woodlands of the Northwest Territories, Canada[1]

E. A. Johnson[2]

Abstract - -Evidence from 10 years of fire records and 300 years of tree ages and fire scars indicate that forest fires in a large area east of Great Slave Lake, N.W.T. are recurrent over a short time interval (<125 years) and related to large scale air mass climate patterns and terrain roughness.

Reconstruction of fire recurrence for 3700 years from paleoecological evidence of treeline position suggests two levels of environmental dynamics. The shorter term change is related to periods of stationary fire frequency and the longer term change is related primarily to climatic change and site conversion. These two levels of dynamics are also observed in the gradient analysis of the contemporary vegetation. The gradients are fire frequency-intensity and topographic-nutrient-energy budget.

INTRODUCTION

First I must warn you that I am not primarily interested in fire history, but instead in exploring the implications of disturbance frequency on the concepts of plant community assembly and dynamics. The arguments I will develop are two: First, fire is a *characteristic*, *frequent* and *recurrent* part of the subarctic lichen woodlands of western Canada. Second, incorporation of these three points requires significant changes in many existing ideas of plant community organization and dynamics.

FIRE RECURRENCE

In northwestern Canada (N.W.T., Saskatchewan and Manitoba) the northern boreal forest forms a transition zone to the tundra. This transition zone varies in width from 400 km in northern Manitoba to less than 100 km south of the Mackenzie delta. The studies herein summarized are located in a 105,000 sq km area (approximately the size of the state of Ohio) east of Great Slave Lake and between 60°N and treeline. The area has about 250 inhabitants mostly in one settlement. There are no roads; access is by float-plane, boat, dog team and snowmobile.

The bedrock is precambrian igneous and metamorphic. The glacial till is generally thin with much bedrock exposed. The region has a humid continental climate with short cool summers, long cold winters and with slightly more precipitation during summer than winter. A characteristic which separates this region from the comparable transition zone in the eastern boreal forest is its low precipitation. For example, Fort Reliance, N.W.T. receives 21 cm precipitation while Knob Lake, Quebec receives 70 cm. Permafrost is not common except in the few lacustrine soils and in peatlands.

The upland canopy vegetation is an open, park-like mixture of jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), white spruce (*P. glauca*) and paper birch (*Betula papyrifera*). The ground cover is predominantly lichens (*Stereocaulon*, *Cetraria* and *Cladonia*) and ericaceous shrubs (*Ledum*, *Vaccinium*, *Empetrium*). The peatland vegetation is generally dominated by open forests of black spruce with infrequent tamarack (*Larix laricina*). Treeless peat plateaus covered with *Cetraria* and *Cladonia* are common. For a flora of the region see Jasieniuk and Johnson (1979).

Our knowlege of forest fires for this area comes from three sources: actual records of forest fires since 1966, forest ages and fire scars for the last 300 years and paleoecological records in peat stratigraphy for the last 4000 years.

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[1] Paper presented at the Fire History Workshop, Oct. 20-24, 1980, Tucson, Arizona.

[2] E. A. Johnson is Assistant Professor of Biology, University of Calgary, Calgary, Alberta, Canada. Manuscript preparation was aided by grants from the National Sciences and Engineering Research Council of Canada and the Boreal Institute.

The forest fire records kept by Northwest Lands and Forests for the decade 1966 to 1975 indicate that lightning caused 87% of the fires and burned 99% of the area burned (figure 1).

Figure 1.--51,000 hectare lightning fire in lichen woodland.

Lightning fire incidence follows a seasonal pattern advancing towards treeline from May to July and retreating from July to September. The July boundary between presence and absence of fires is approximately treeline (Johnson and Rowe 1975). This seasonal pattern of forest fires seems to be related to conditions associated with the maritime Pacific air mass either along fronts with the continental Arctic air mass or in isolated convective systems (see Bryson 1966 for air masses and treeline). As a result fires decrease in frequency and size towards treeline (figure 2).

Years in which there are few fires are related to above-normal precipitation during the summer fire season. This above-normal precipitation keeps the duff moisture at a level which will not support fires. Meterologically the above-normal precipitation results from an anomalous surface water temperature pattern in the north Pacific. This anomaly gives rise to an amplified atmospheric long (Rossby) wave which increases the convergence along the contact between the maritime Pacific and continental Arctic air masses in the N.W.T. In general the yearly oscilations in fire numbers and area burned are correlated: severe fire years to low zonal indexes of westerly flow in the atmosphere and mild fire years to high zonal indexes.

Forest ages and fire scars can be used to extend our understanding of the frequency and pattern of forest fires back about 300 years (Johnson 1979). The method consists of determining the burning "mortality" within each of four

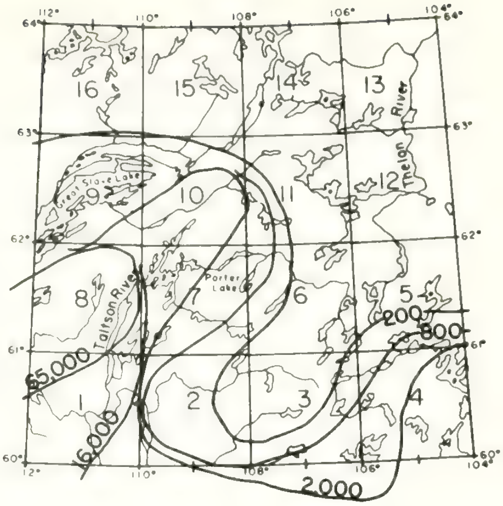


Figure 2.--Isolines of fire size (acres) expected to recur on the average every two years (For method of construction see Johnson and Rowe 1975).

regions (25 to 100 km^2). In each region, 15 to 36 upland stands of approximately 10 ha were located on a map grid using random numbers. All regions sampled had burned within the last four or five years, so that the age intervals would represent fire-to-fire events. The intervals between fires for each stand were determined from an investigation of fire scars and tree rings. There was a good fit ($\alpha = .01$) between the observed intervals between fires (t) and those predicted by the "mortality" distribution:

$$f(t) = \frac{dF(t)}{dt} = \lambda(t)\ P(t) \tag{1}$$

where $P(t) = \exp -(t/b)^c$ is the site surviorship and $\lambda(t) = c/b\ (t/b)^{c-1} = -1/P(t)\ dP(t)/dt$ is the hazard of burning. $\lambda(t)dt$ is the conditional probability of burning in the interval $(t, t + dt)$. This "mortality" distribution has two parameters. The expected recurrence time of fire (b) gives the interval between fires which has the highest probability of occurring. The shape of the mortality distribution (c) gives the variation around the expected recurrence. If it is 3.6 the distribution is normal, if it is < 3.6 the distribution is positively skewed and if it is = 1 the distribution is monotonically decreasing (figure 3).

The expected recurrence time (b) is related to the regional aspects of the environment which are related to fire ignition and spread. Figure 4 shows that this parameter increases (time between fires increases) as the sampled regions get closer to treeline. This is similar to the pattern found in the 10 years of fire records as shown in figure 2.

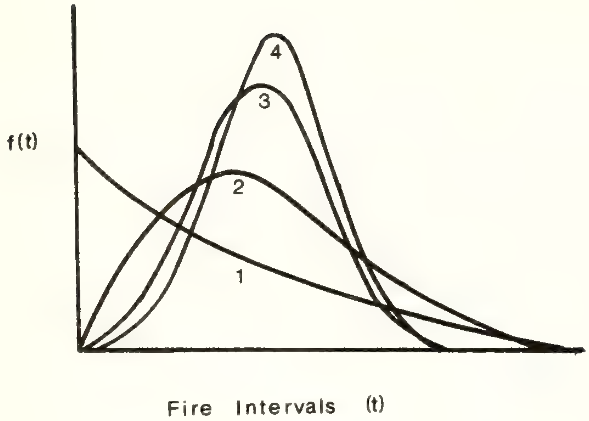


Figure 3.--The fire frequency "mortality" distribution of equation (1) with different values of the shape parameter c.

The burning of a population of sites is affected not only by their shared regional environment, such as the air mass climate, but also by individual differences between sites such as terrain, vegetation and topoclimate. The shape parameter (c) indicates this variation. In smooth terrain the variation in the fire environment between sites in the population is due largely to chance, and the variation around the expected recurrence time is symmetrical (c ~ 3) in the mortality distribution. In rough terrain the variation around the expected recurrence is positively skewed (c = 1 to 3). The tail of the skew indicates the existence of a few sites which survive fires much longer than most others.

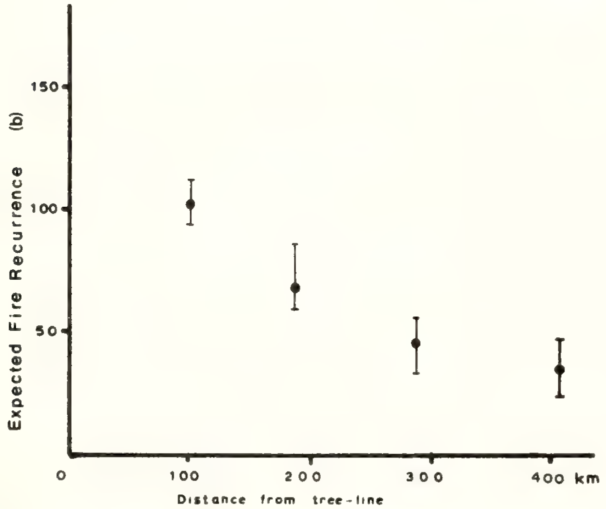
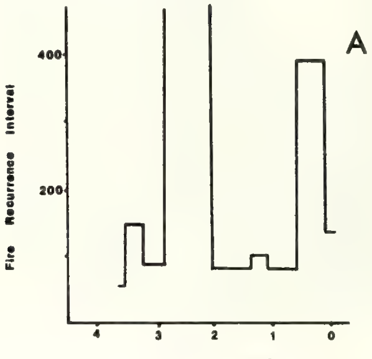


Figure 4.--The expected fire recurrence interval (in years) decreases as one moves away from treeline. Compare this to the similar pattern in figure 2. Bars represent 90% confidence intervals.

It is possible to speculate about the fire recurrence for nearly 4000 years by using paleoecological evidence. Sorenson *et al.* (1971) and Nichols (1976) present reconstructions of the forest/tundra boundary in this region from radiocarbon dates, paleosols and pollen analysis. These reconstructions give the age and distance of the present forest/tundra boundary from its positions in the past. By using this information and the relationship of fire recurrence to distance from treeline (figure 4), a reconstruction (figure 5A) can be made of the fire recurrence intervals for 3700 years in the Porter Lake regi (see location in figure 2).



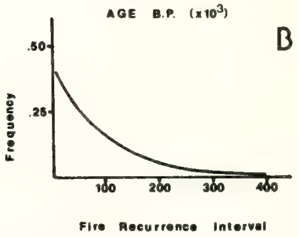


Figure 5A.--Tentative reconstruction of fire recurrence at Porter Lake, N.W.T. for 3700 years. Based on paleoecological evidence for position of forest/tundra boundary and the contemporary relationship of fire frequency and treeline. The step changes in the recurrence are due to the relative discreteness of the climatic changes; the curve would be smoothed if the lag response of vegetation and soil were considered.

Figure 5B.--Frequency of fire recurrence interval for 3700 years at Porter Lake.

Two levels of environmental dynamics can be hypothesized from this reconstruction of fire recurrence at Porter Lake. First, a shorter term dynamic occurs during which the fire frequency is stationary. This period may include one to many fire-vegetation recovery couplets, with each stationary period lasting from 300-1000 years. Between these stationary periods are transitional intervals during which the fire frequency and other environmental parameters change rapidly. These singularities are usually associated with change in the atmospheric circulation. This longer term dynamic seems to occur randomly because the density distribution (figure 5B) follows a negative exponential.

Demonstration that forest fires are *aracteristic, frequent* and *recurrent* in this rt of the subarctic has some immediate consuences for the understanding of vegetation namics in the subarctic.

The survivorship of sites indicate that 50% 11 have burned by the ages of 60 to 100 years. om the point of view of the major tree species *icea mariana, P. glauca, Pinus banksiana*), which n live to be 300 or 400 years old, death will obably occur by fire well before this maximum e is reached.

The high fire recurrence creates real dif-culty for traditional arguments of succession d climax. Firstly, if 300 or more years are quired to reach the postulated black spruceather moss climax (cf. Kershaw 1977) then there simply not enough time between fires for the imax to develop except in very rare cases. condly, the evidence is convincing that the re frequency is primarily determined by the air ss climate. Consequently it is difficult to gue that the fire frequency is for some reason tifically (e.g. man caused fires) or abnormally gh and that this is preventing the "natural" ccession.

VEGETATION ORGANIZATION & DYNAMICS

The two environmental dynamics of figure 5 re also reflected in a gradient analysis of the ntemporary vegetation as shown in figure 6 (cf. hnson 1980).

The habitat gradient in figure 6 is associated with topographic - nutrient - energy budget actors. These factors remain relatively constant n influence because of the stability of aspect, lope and substrate types. A stand's environental factors which locate it on the gradient, ill change significantly only during the singular eriods usually associated with changes in climtic regimes and sometimes with geomorphic hanges, pedogenesis, species invasion or extincton and introduction of pathogens. The habitat radient is the longer term dynamic of figure 5. t represents the major changes in species compsition usually associated with changes in commnity type classifications.

The fire frequency and intensity gradient n figure 6 describes an environmental factor fire) which is recurrent but acts quickly and hen stops. It interacts slightly with the habiat factors (as is indicated by the non-orthogonal elation of the communities) because the destructon of the vegetation canopy leads to a more egative ("cooler") energy budget for 30 or 40 ears (Rouse 1976).

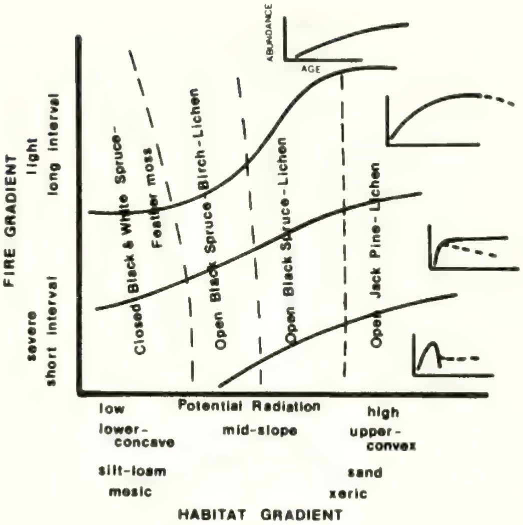


Figure 6.--Gradient Analysis of upland vegetation along the two major environmental gradients. The habitat gradient is related to topographic-nutrient-energy budget factors while the fire gradient is related to fire frequency and severity. Community types are characterized by the most abundant canopy and understory species. The small graphs on the right indicate the predominate fire recovery pattern depending on the location in the fire and habitat gradient.

The fire frequency and intensity gradient s the shorter term dynamic of figure 5. Species an persist and/or recover from fires only when heir life histories are in some manner correlated to the recurrence interval and severity of the fires (Johnson 1980). Since plant communities consist of a spectrum of species with varied life histories, community response in terms of structure and composition will reflect the selection of those species adapted to the fire interval and severity (see figure 6). Consequently as long as the recurrence is short relative to the life span of the species and stochasticly stable, most species present before the fire are present shortly afterwards. This is a result of vegetative reproduction from surviving parts and diaspores e.g. spruces (seed), jack pine (seed) and lichens (fragments and soredia).

Changes in vegetation composition implied in many fire recovery successions (e.g. Scotter 1964) are due to differences in conspicuousness resulting from different growth rates and size-density relationships (Harper and White 1974). The sequence often described of birch being replaced by spruce is primarily due to differences in growth rates, not age and establishment differences; similarly for jack pine to spruce and *Cladonia graclis* to *C. mitis* to *C. rangiferina.* Also recovery sequences often confuse the habitat gradient with the fire gradient.

CONCLUSION

The vegetation landscape of the western subarctic lichen woodland consists of two overlain and interactive mosaics, one related to habitat differences and one related to fire. The habitat mosaic is the major organizing force on vegetation composition and structure, accounting for changes in the kinds of species adapted to different sites. Overlying this mosaic is the change in vegetation abundance resulting from the selective influence of the interval between and severity of fires. Both mosaics interact. The habitat factors influence, for example, the amount of biomass accumulation (fuel) and fire climate of a site while fire influences the seed bed (fire intensity) and the site's energy budget (intensity and frequency).

The dynamics of these two sets of environmental factors does not lead to any developmental succession of communities. Developmental succession, as usually conceived by ecologists, would not lead to a reliable reconstruction of communities (with a maximum persistent biomass and relatively closed nutrient cycling) after disturbance by fire or habitat changes. This reliability can only be obtained by highly individualistic populations (varied life histories) which as units can be disintegrated and reconstituted in a variety of combinations without loss of the above mentioned stability.

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Hunter-Gatherers and Problems for Fire History[1]

Henry T. Lewis[2]

Abstract.--Reconstructing fire histories in regions where hunting-gathering peoples once used burning techniques appears to present special problems of interpretation. Studies over the past two decades involving the reconstruction of indigenous firing practices in western North America and observations of extant practices in northern Australia indicate some of the major difficulties involved.

The tropical savanna region of northern Australia is one of the few areas of the world where indigenous peoples still use fire to modify local habitats to manipulate the distribution and relative abundance of hunting and gathering resources. Recent studies in Arnhemland, Northern Territory, have shown the importance which these practices have for managing a range of subtropical ecosystems.[3] Though these practices apply to a markedly different environmental zone than any of those which have been considered during recent years in western North America, the overall strategies employed by Aborigines and Indians are remarkably similar.[4] Of special importance for understanding fire histories in the two regions, the argument is here made that the variable ways by which Aborigines and Indians employed fire resulted in difficult, in some instances insurmountable, problems of interpretation for studies of fire histories.

The problem essentially derives from the fact that hunters and gatherers employ patterns of burning which are significantly different from natural patterns of ignition and, with both man-made and natural fire regimes occurring throughout a given region and range of micro-habitats, information derived from fire scars may provide little real insight into the chronology and frequency of fires. The central problem can be seen with the major technological considerations that hunting-gathering societies use in their respective fire technologies: the seasonality and frequency of burning, the intensity and size of fires, and the ways in which fires are applied (or alternately withheld) in different habitats. Paradoxically, it is the very ways in which prescribed burning has been used that accounts for its environmental importance and the paucity of fire scar evidence.

Indigenous fire practices in North America have been quite literally extinguished and our interpretations of the patterns once involved and the impacts made are based on historical records or, in a very few cases, recall data provided by older informants from isolated areas where burning technologies were employed until forty or more years ago (Lewis 1977, 1981b). Though oral histories are potentially far more useful than documented source materials--which most frequently do little more than confirm the fact that Indians did burn--neither provides the empirical detail that ongoing, contextual studies would reveal.

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[1] Paper presented at the Fire History Workshop. (Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980).

[2] Henry T. Lewis is Professor, Department of Anthropology, University of Alberta, Edmonton, Alberta, Canada.

[3] Reports on contemporary uses of fire by Aborigines in northern Australia are now beginning to appear in print and further studies are in progress. The first to deal with the subject was Jones (1975) who, in a subsequent work (1978), has incorporated the uses of fire into more general practices of hunting-gathering technology in northern Arnhemland. Three papers dealing specifically with fire uses can be found in the work of Haynes (1978a, 1978b, 1978c); these are especially significant papers regarding the practices and beliefs of Aborigines in central Arnhemland. The substantive materials described in this paper derive from Haynes' work plus, on a more personal level, information and assistance that he provided the author while in the Northern Territory from mid-June to mid-August, 1980. A series of unedited discussion papers (Fox 1974) offer a range of comments by social scientists and biologists on Aboriginal uses of fire in the north. Still other writers on the Northern Territory have commented on the use and possible significance of Aboriginal practice (Davidson n.d., Peterson 1971, and Stocker 1966). Considering the dearth of materials on the contextual employment of fire by hunter-gatherers in other parts of the world, the materials on northern Australia are comparatively rich.

[4] Studies on Indian uses of fire have included works by Arthur (1975), Barrett (n.d.), Boyd (n.d.), Bean and Lawton (1973), Day (1953, Lewis (1973 et al.), Reynolds (1959), and Steward (1951 et al.).

Fortunately, important comparable data concerning extant fire technologies can still be derived from areas like northern Australia and like situations in isolated parts of Africa and Asia. In this respect the Arnhemland studies are especially significant because for the first time we have field studies on the uses of fire by hunting-gathering peoples. These examples are further important foı what they suggest about functionally similar conditions in North America.[5]

The seasonality, frequency, intensity, scale, and type of Aboriginal fires in Arnhemland vary significantly between vegetational communities and from one micro-habitat to another. Within the four major vegetational types of the Northern Territory's savanna region--monsoon forest, open floodplains, tall-open forest, and eucalypt woodlands--firing activity begins in mid-April with the onset of the dry season, continues virtually on a day-to-day basis for approximately four months, and then sporadically in some areas until as late as mid-December and the return of monsoonal rains. Each area, however, is managed in distinct ways.

For the monsoon forest stands (deciduous vine thickets and semi-evergreen vine forest areas which are seldom more than 10 ha) particular care is taken to exclude fire, if at all possible. Because monsoon forest vegetation can sustain severe damage from late, dry season fires (Stocker and Mott 1978), the surrounding drier grass margins of floodplains and the grass and shrub understories of tall-open forests are burned early in the dry season to create firebreaks. Reasons for excluding fire from monsoon forests include a combination of practical considerations (especially to protect the vines of yams) and important totemic-religious beliefs.

In marked contrast, nearby floodplains are fired at virtually any time between mid-April and early August with as much as 90% of these grasslands burned in a given year. Mainly in growth to various species of *Cyperaceae* and *Gramineae* these coastal floodplains are inundated for the several months of rainy season. Burned for both the small animals killed in such fires and the secondary green-up that follows, more animals are soon drawn from surrounding vegetation types to feed there.

Further removed from the coasts, in areas receiving 750 mm or more annual rainfall, the tall-open forests are dominated by evenly spaced eucalypts (esp. *E. tetrodonta* and *E. miniata*) of from 18 to 24 m high and an understory of grasses (particularly *Sorghum intrans*) and shrubs, the densities of which are largely determined by the frequency of burning. Though sporadic burning begins by mid-April, most burning within open forest areas takes place in the two-month period of mid-June to mid-August. Though individual fires are small (1-5 ha) and discontinuous, Haynes (1978b estimates that between 25% and 50% of the tall-open forests are burned in a given year. An important feature of controlling these fires involves making use of the relatively high winds (25-35 k.p.h.) which occur during the two months. This condition is important to Aboriginal burning technology in that fires are more easily directed (e.g, burning into previously fired patches or natural firebreaks and scorch height is consequently lower, thereby causing less damage to the flowers and buds of important fruiting trees. Related to this is the added controlling factor that winds drop off late in the day and fires go out at night during this cooler period.

The overall effect of this more-or-less annual frequency of burning is to create a mosaic of unevenly aged understory plants. Some areas are fired every year, others less frequently, with many burned portions overlapping from one season to another depending upon the particular clusters of plants and the actual extent and intensity of fires in a particular place. The trees of tall-open forest are seldom killed by fires at this time (unless already aged, diseased, or termite infested) nor are they frequently or consistently scarred because of the relative low intensity of the fires.

The fourth environmental zone is the eucalypt woodland, a savanna forest with a lower diversity of plant and animal species than that found in tal open forest areas. Usually dominated by *E.* dichromoploia, and with large numbers of *E. miniat* and *E. tetrodonta*, these drier (less than 750 mm per annum) and more open regions (the trees more widely spaced and usually less than 12 m high) are characterized by understory fires that are larger and more intense. Though the overall floral and faunal diversity is less than that of tall-open forests, eucalypt woodlands are the preferred cattle grazing areas of the north, supporting two-to-three times the number of stock found in tall-open forest regions (Perry 1960).

However, partly related to the emphasis which hunting-gathering societies place upon a wide spectrum of plant and animal resources, the more uniform eucalypt woodlands are viewed by Aborigine in Arnhemland as "desert" or "rubbish country" (Haynes 1978b and personal communication), primari mportant for the animals taken when using fires s a direct hunting technique, and subsequently or the macropods attracted by the "green pick," r green-up that follows early season burning. As ith the tall-open forests, the pattern of burning s patchy but both burnt and unburnt areas are arger. Also, fires are ignited in eucalypt woodands over a longer period of time than in other reas: from the end of the wet season, through ugust, and into the weeks immediately prior to he onset of monsoon rains in mid-December. Thus, s a less important zone for Aboriginal economies, urning practices within eucalypt woodlands are arried out much more casually and with less concern or local plant and animal associations. As with ther areas, the time of year, frequency, and elated conditions influencing the intensity of urning have a considerable effect upon the extent nd regularity of scarring.

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[5] Except for observations noted in a recent report to the Australian National Parks and Wildlife Service (Hoare et al. 1980:46), there are no published references on northern Australia concerning fire scarring. The interpretations made here derive from the author's own observations and, more significantly, the observations of individuals who have worked for a number of nears on related problems of fire effects in northern Australia. Among the people to whom the author is particularly indebted are Chris Haynes (Australian Parks and Wildlife Service, Darwin) and Dr. M. G. Ridpath (Division of Wildlife Research, Commonwealth Science and Industrial Research Organization, Darwin).

For example, over the past hundred years the pastoral industry in the Northern Territory has used fire extensively as an aid in mustering cattle--for both clearing the 2-m high grasses and initiating new, palatable growth, the "green pick," to attract stock. Cattlemen, in contrast to Aborigines, attempt to burn eucalypt woodlands as early as possible (between mid-April and mid-June) to obtain the maximum amount of new growth so that stock will have at least a minimum amount of nutritious feed until the return of the wet season. Though stockmen burn larger areas, and do so on a more regular-annual basis, trees are scarred less frequently, it was suggested, because fire intensities are reduced at this time and, in burning areas more regularly than do Aborigines, fuel loads are kept down.

The natural fire regime of the Northern Territory's "Top End" derives from thunderstorms occurring in the months immediately preceeding monsoon rains. However, given the effects of man-made fires and the consequent reduction of fuels, lightning fires rarely occur (Stocker 1966). With monsoon forests that are fire protected, tall-open forests of which up to 50% are burned in small, discontinuous patches over a two-month period, grasslands which are almost completely fired each year, and eucalypt woodlands which are fired more or less indiscriminately throughout the dry season, the results of Aboriginal fire management are highly variegated. Northern researchers were unanimous in their agreement that the fire scar evidence from essentially man-made fire regimes was quite inadequate for reconstructing the complex of pyro-technical events--either Aboriginal or Euro-Australian in origin.

As Haynes' definitive studies show (1978a, 1978b, 1978c), the pattern of Aboriginal burning is quite clear when examined firsthand. However, it is a pattern that does not result in equivalent, discrete types of evidence. In fact, it is partly designed to avoid the kinds of perturbations that result from lightning fire regimes. The result is that in themselves fire scars provide no insights into the complex of man-made fire dynamics in northern Australia.

In the case of North America we unfortunately have no extant situations involving hunting-gathering burning practices. Though there are still remote areas of Canada and Alaska within which burning was carried out until recent times, and where some aged informants are still available, most of our information is derived from incidental historical references. However, despite the lack of contextual studies, there are general patterns which emerge (Lewis 1981a), and these suggest similar difficulties for interpreting fire scar evidence in regions where Indians once employed prescribed burning.

Like Aboriginal hunters and gatherers of Australia, North American Indians used fires in ways that differed significantly from natural fire patterns, especially in terms of the major considerations involved: the seasonality and frequency of burning, the intensity and scale of fires, and the kinds of fires used. In the same ways that there are great variations in the regional uses of fire within Australia (Nicholson 1980), specific practices varied from one habitat and one zone to another given the importance of the resources involved.

In an area from which we have our most detailed information on North American Indian practice, northern Alberta, burning was mainly confined to grasslands and, according to informants, extended areas of boreal forest were left unburned (Lewis 1977, 1981b). Unlike those Indians of California who set autumn ground fires within the ponderosa-sequoia forests, Indians of this subarctic region did not (could not) employ understory burning within the boreal forest. Except for the early spring burning of deadfall and windfall areas (Lewis 1977:40), fires within the boreal forest were apparently the consequence of lightning storms and human carelessness throughout late spring and summer. Thus, unlike the savannas of northern Australia, lightning fires undoubtedly did play a significant role in northern Canada.

However, it appears that the combination of man-made and natural fires in the northern boreal forest would have resulted in a greater diversity of variously aged communities than is now the case. In the absence of light understory fires the evidence from fire scars probably presents a more reasonable record of natural fire frequencies within forested areas than is the case for other vegetational types. However, it can tell us little if anything about the effects and counter-effects which the Indian burning of intervening grasslands and shrub areas, resulting in a more pronounced forest mosaic, might have had for limiting larger, more destructive fires.

In California's regions of prairies, oak-grasslands, chaparral, and montane forests, prescribed fires were carried out in variable ways that related to the distribution and relative abundance of plants and animals in each zone. The overall result, I have argued elsewhere (Lewis 1973), was to create a more diversified environment and one that was less susceptible to the major disruptions which are now more characteristic of natural fire regimes.

The central prairies of California and Oregon (Boyd n.d.) were burned in late summer of each year to initiate a second green-up of grasses, with the frequency of burning acting as the primary factor for controlling fires.[6] Chaparral areas were burned so as to maintain grass openings, with older chaparral being periodically fired to maintain clearings and ecotones between grasses and shrubs. Depending upon specific resource goals and variations in habitat (e.g., south-facing chamise and north-facing mixed chaparral), fires were ignited in both fall and spring. Within the coniferous forests of the Sierra Nevadas, fires were set underneath trees whenever sufficient fuel buildups developed, a pattern very similar to that carried out by Aborigines in the tall-open forests of northern Australia. The problems which exist with correlating fire scars from such an area may, in part at least, be attributed to the high frequency with which Indians actually burned, a frequency higher than the "adjusted" fire scar evidence suggests.

The growing number of studies from Australia and North America are now beginning to demonstrate the considerable importance which indigenous burning practices had for environments in these two different parts of the world. And, even though so much information is now lost to us, the fact that we have technologically parallel examples from a number of environmental zones in two continents strengthens the overall argument for the importance of human interference in affecting fire histories. A failure to consider the major factors, the human artifacts involved (the seasonality and frequency of burning, the scale and intensity of firing, plus the ways in which fires were set or excluded) make conclusions drawn only from fire scar data problematic at the very least.

Over the past two decades anthropologists have increasingly moved away from the isolation of considering only social and cultural questions to include a wide range of perspectives and information from environmental sciences in order to broaden their interpretations of human adaptations. On the basis of questions raised here, I think it not inappropriate to suggest that whenever possible studies of fire history must include all available information regarding known practices of hunters and gatherers as they influenced plant and animal communities with fire (e.g., Barrett (n.d.)). Though this will enormously complicate interpretations, the pictures to emerge will provide much more towards an understanding of the dynamics of environments as they have been influenced by humans for past millenia. It is not enough merely to note that Indians or Aborigines set fires. It is especially important that we begin to understand the variable but locally specific impacts which these fire technologies have had in the human history of fire.

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[6] An exact parallel of this technique has been described for Western Australia by Hallem (1975).

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Forest Fire History: Ecological Significance and Dating Problems in the North Swedish Boreal Forest[1]

Olle Zackrisson[2]

Abstract.--The past and present fire regimes are described, and the significance for the flora of this region is discussed. Methods used to reconstruct forest fire history are presented. The dating problems with false and absent rings in Scots pine, Norway spruce and two birch species are also dealt with.

INTRODUCTION

Descriptions of fire impact on the Swedish forest landscape are often found in literature from the 18th and 19th century. Already at that time fire was considered to have a purely negative effect, and fire prevention was considered desirable. This opinion found expression in the legislative measures taken to stop or prevent any use of fire to modify the forest ecosystem for agricultural practice.

At the end of the 19th century and the beginning of the 20th century, when the first more comprehensive forest biological research was carried out in North Sweden, the importance of fire for the origin and stability of the forest types was often discussed (Holmertz & Ortenblad 1886, Tamm 1920). The destructive influence of forest fires was very much stressed and a special forest organization was founded with the aim or reducing the impact of fire on the forests in the north of Sweden. Later, when the influence of uncontrolled fires was reduced, scientists tended to underrate the importance of fire as a natural ecological factor throughout history. Forestry research appears to have stressed man's role in causing forest fires, and often neglected or even denied the fact that many were caused by lightning.

Interest in fire ecology was greatly increased by the extremely severe fire year of 1933, and some very interesting work was consequently done (Högbom 1934, Wretlind 1934, Tiren 1937). Since the close of the 1930's very little research has been carried out on the natural importance of forest fires. One exception is the study by Uggla (1958) of a burned forest area in the Muddus region, North Sweeden. Recently, a further series of papers on fire ecology of the whole circumpolar area has stimulated a fresh approach to, and renewed interest in, reconstructing fire influence on the boreal forest. The negative attitude toward the use of fire as a suitable management method for virgin-forest reserves has very slowly begun to change as knowledge of its actual function in ecosystems has increased. A more positive approach to the use of fire in modern forestry to improve regeneration by prescribed burning on soils with a thick, raw humus layer is also now detectable.

It is not until now that we have begun to realize how frequently the North Swedish boreal forests have been subjected to forest fires, and what effects they have had on the organisms found there.

CHANGES IN THE FIRE REGIME AND ITS SIGNIFICANCE FOR FOREST VEGETATION

Investigation of the forest region in the Vindelälven Valley, North Sweden has shown a forest fire rotation of about 100 years from the end of the medieval period up to the close of the 19th century (Zackrisson 1977). This figure includes different types of forest found within the whole river valley.

The Scots pine (Pinus sylvestris) dominated forest found on glaci-fluvial sandy plains along the river, has burned most frequently with a mean fire interval of about 46 years (fig. 1). In local stands, mean fire intervals of approximately 30 years for the last 600 years are found in the most fire-prone areas. Fire in this type of forest often gave rise to very uneven-aged stands, where successful regeneration often occurred a short period after the last fire.

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[1] Paper presented at the fire history workshop (Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980).

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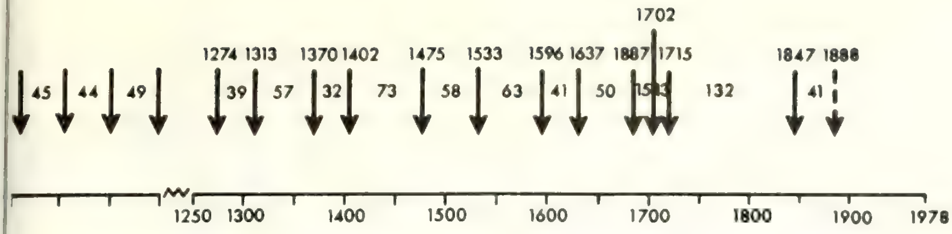


Figure 1.--Local forest fire chronology of a lichen-pine forest stand in Harads, North Sweden. The fire years are marked with arrows and the intervals between fires are shown by figures between the arrows. The floating chronology to the left goes into the Viking age, but does not correspond exactly with the absolute chronology because of problems with absent rings in the oldest samples. The chronology is built up from 81 crosssections of pine. A mean fire interval of about 50 years is rather typical for most lichen-pine forests in the interior of North Sweden.

In mixed coniferous stands of the Vaccinium type found on morainic soils, intervals between fires are usually longer. Mean fire intervals are commonly 100 years. In this type of forest, Norway spruce (Picea abies) often forms the undergrowth regenerated after each fire. Scots pine often survives as overstory trees and can reach old ages (fig. 2).

In all these forest types previously influenced by frequent forest fires, fire impact has decreased drastically during the last 100 years (Zackrisson 1977). This is partly a consequence of severe restrictions in the rights of burn-beating and of burning for grazing improvement, as well as the introduction of an active fire-prevention policy. The latter received active support from the bulk of the population as soon as the value of forest for timber production was acknowledged.

Another very important factor in decreasing fire frequency was the passive fire elimination caused by extensive cutting out of dead standing trees from the 19th century and onward. Dry snags are of particular importance with regard to forest fires caused by lightning, since they catch fire much more readily than living trees do (Kourtz 1967).

In spruce forests on wet sites, fire has usually been rare. Fire-free intervals of up to 500 years can be found in exceptional cases. Normally, this type of long-term fire-free refuge seems to be a rather rare phenomenon in most of the boreal landscape. The special environment found in this type of late successional stage seems to be favorable for some very rare arboreal lichen species (Essen et al in press). Some rare vascular species could also be expected in the very late successional stages. It is important that such natural refuges be found and protected from clear-cutting, because several threatened species may be adapted to them.

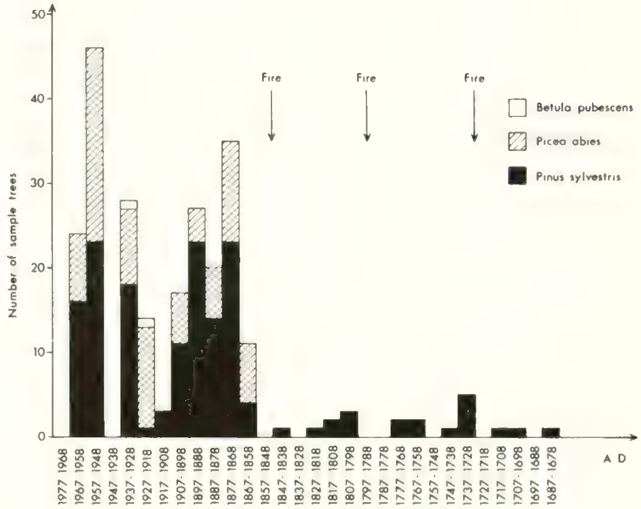


Figure 2.--Reconstruction of forest fires and successful regeneration in a mixed coniferous stand with overstory trees of Scots pine and undergrowth of Norway spruce. Spruce is sensitive to fire and all regeneration of spruce has come after the last fire. The regeneration during the last 70 years is also influenced by selective cutting of Scots pine. Sample plot 50x 20m, Arvidsjaur, North Sweden. Trees under breast height were not dated.

Unfortunately, we have the same lack of knowledge concerning species dependent on frequent fire disturbance. There is therefore a great need for investigations describing different fire adaptations found among organisms in the boreal forest. By studying the strategies and mechanisms developed by different species to survive the long-term influence of repeated fires, we probably also will improve our understanding of floristic and faunistic changes currently taking place.

Some of the dynamics found today could be a direct effect of the drastically reduced influence of forest fires in the landscape. Organisms adapted to the special environment created by repeated fires may not always have been able to find other suitable sites for their survival, and so decreased both in number and distribution. To reduce these effects, a reintroduction of boreal pyro adaptions, as well as knowledge of the previous long-term influence of fire on different parts of the boreal landscape, is however very fragmentary. More detailed information is needed before fire can be

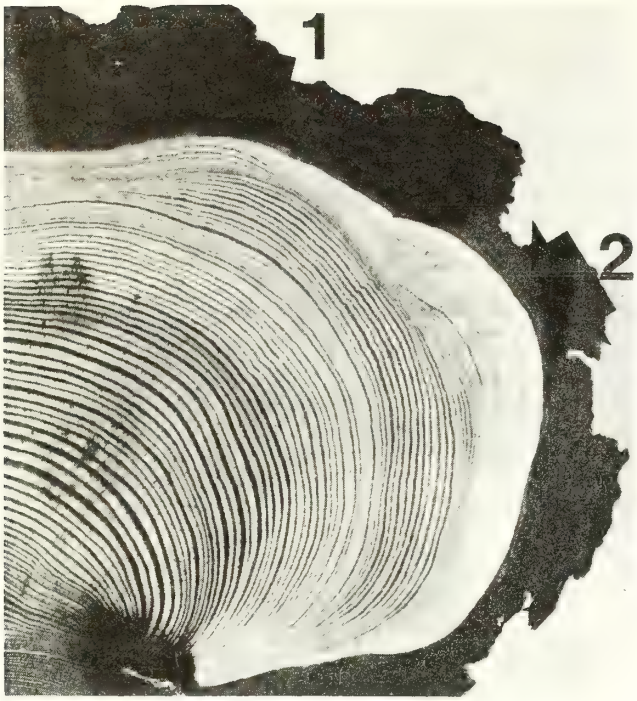


Figure 3.--Overhealing wood close to a fire scar in Scots pine. A ring count made from a bore core in direction 1 would have given 24 rings less than a count made in direction 2, because of partial absent rings. Disappearing rings are a serious problem when bore cores are used for dating, but could in most cases be avoided when well-prepared cross sections are used from different levels of the scar.

reintroduced in full scale as a management tool in nature conservation.

METHODS OF RECONSTRUCTING FIRE INFLUENCE ON THE FOREST

Historical sources such as land survey maps, court records, records of land inquiries, annual reports from district forest officers, and travel descriptions can be used to reconstruct the previous influence of fire on the forest landscape of North Sweden. These historical sources can be used to reconstruct burned areas and to check if the dating of a particular fire made by tree-ring counts is correct. Forest fires from this century can be traced by fire registrations at each fire fighting district.

For a detailed reconstruction of the fire history on a particular forest site, fire scar-dating is the easiest method to employ. In the forests of North Sweden, Scots pine can reach ages close to 1,000 years (Zackrisson 1979). Pine trees with multiple fire scars are common in areas less influenced by previous logging operations. Virgin forest types with Scots pine are also mostly quite uneven-aged, which is favorable when dendroecological methods are used to study the previous fire regime. In the interior of North Sweden, dry standing trees, and stumps and logs on the groun are often well-preserved from rot because of the more continental climate found in this region. Dea wood of this type can be used for fire dating purposes (Zackrisson 1976).

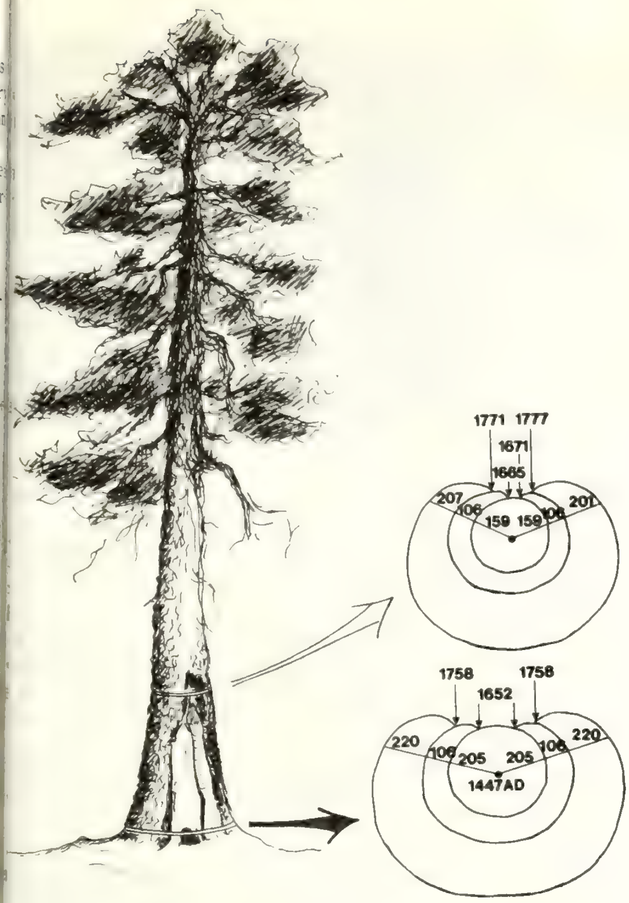
Scots pine has traditionally been believed to produce annual rings even under very severe environmental conditions. This is probably true in most cases. The problem with partially absent rings, however, seems to be overlooked (fig. 3). When a cross section is taken, this problem can be eliminated in most cases, but when only a bore core is available, the problem is more serious unless cross-dating techniques are used.

Partial rings seem to be rather common in old low-vigor trees. Cross sections taken at different levels of a pine stem could give different dates for the same fire scar. This phenomenon is described in fig. 4. Cross sections were taken close to the root neck and at breast height (1.3m). Dating by ring counts from the two samples in this case gave two different dates for the fires. The difference is no less than 13 to 19 years. The sample taken at the root neck level shows the accurate date of the last fire in 1758. This fire year has been verified by an extensive reconstruction of the forest fire history of the area. It is uncertain if this is more general phenomenon found in most tree specie but this should be studied more thoroughly.

Assymetrically developed rings, with sections of numerous rings missing, seem to be rather common in cross sections of Norway spruce and birch from some types of forest sites. An investigation made in a spruce stand in Arvidsjaur, North Sweden, influenced by a well-documented fire in 1831, will illustrate some of the dating problems caused by missing rings. The spruce stand was affected by a surface fire that killed some spruces but left others alive with fire scars at the base of the stem. Due to the fire, the spruce stand is composed of two different age classes. The younger spruces, all belonging to a lower tree layer, regenerated shortly after the fire in 1831.

Spruces with fire scars were sampled to stud ring formation in the wood produced after the fire As a consequence of the extensive fungal infections found in the older spruces previously damaged by fire, great problems arose in getting enough material for this pilot investigation. More than 200 trees with fire scars were cut, but only 24 could be used for ring counts. The cross sections accepted were taken out close to the root neck of the trees. In each cross section the tree rings were counted from three directions (fig. 5) under a Wild M 8 stereomicroscope.

Of the 72 counts made from different directions from the 24 cross sections, only 31 (43%) counts showed the accurate number of rings that should have been produced if one ring was formed annually from the damage in 1831 until



igure 4.--Scots pine from Jokkmokk, North Sweden, scarred by well-documented fires in 1652 and 1758. The cross section taken at the base shows the accurate number of rings, while 13 to 19 rings are missing in the sample taken at breast height. These 13 to 19 rings are lost in the wood formation after the fire in 1758. A date made by ring counts at 1.3m would in this case have given quite incorrect dates for the fires. This is indicated in the figure by the false fire years 1771, 1777, 1671, and 1665.

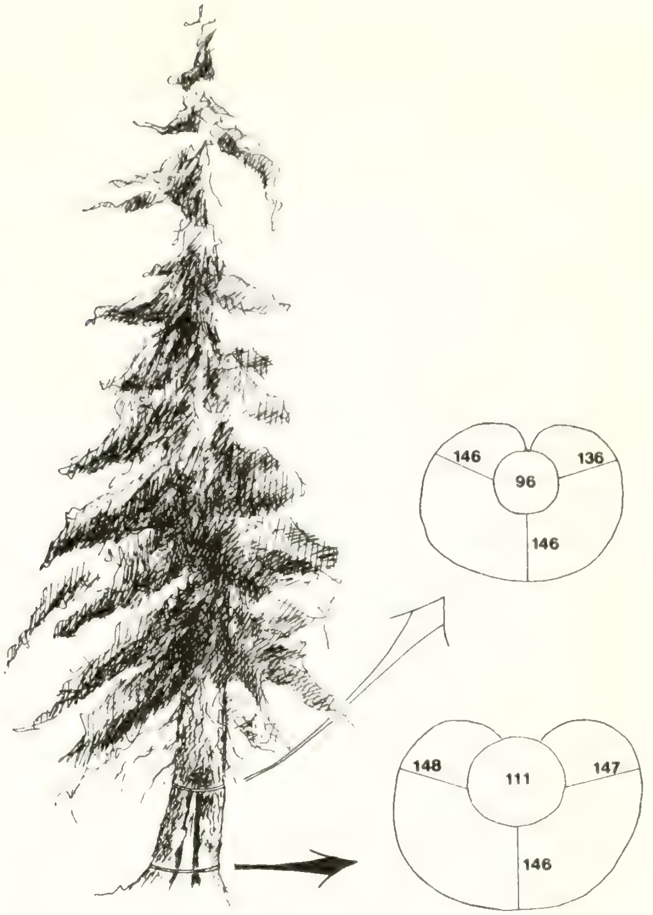


Figure 5.--Norway spruce scarred by a fire in 1831. Ring counts were made at three directions as described in the text. Only one ring count (148 rings) made in the cross section taken out at the base of the stem could verify the actual fire year. The figure shows the rings found at different counts.

1980 (fig. 6). This pilot study also shows that 66% of the error found lies with ±1 year. Four percent of the counts showed more than 10 absent rings. In one observation, 21 rings were absent. When considering the counts with the highest number of rings found in each cross section, only 50% of the sampled cross sections could give an accurate number of rings in all three directions. Only in these trees would it seem reasonable to assume that a core taken out with an increment borer at the base of the stem would provide an accurate date for the fire by counting the rings found in the core.

In some cases, a false ring was produced close to the scar margin (fig. 7). This is also the reason why one extra tree ring is found in some counts in fig. 6. In most cases, this type of ring could rather easily be recognized as false if studied more closely. If studied at a higher magnitude, it mostly gives the impression of a frost-ring. How this type of false ring is formed is uncertain. One explanation is that heat from the fire could damage the xylem mother cells without lethally damaging the cambium. There are indications that xylem mother cells and undifferentiated tracheid cells are more sensitive to extreme temperature than the cambial cells (Aronson 1980).

The false ring formed close to the margin of the scar could, however, have a varying structure and could in some cases closely mimic a real latewood formation with an abrupt transition to earlywood. It seems easy to recognize a false ring

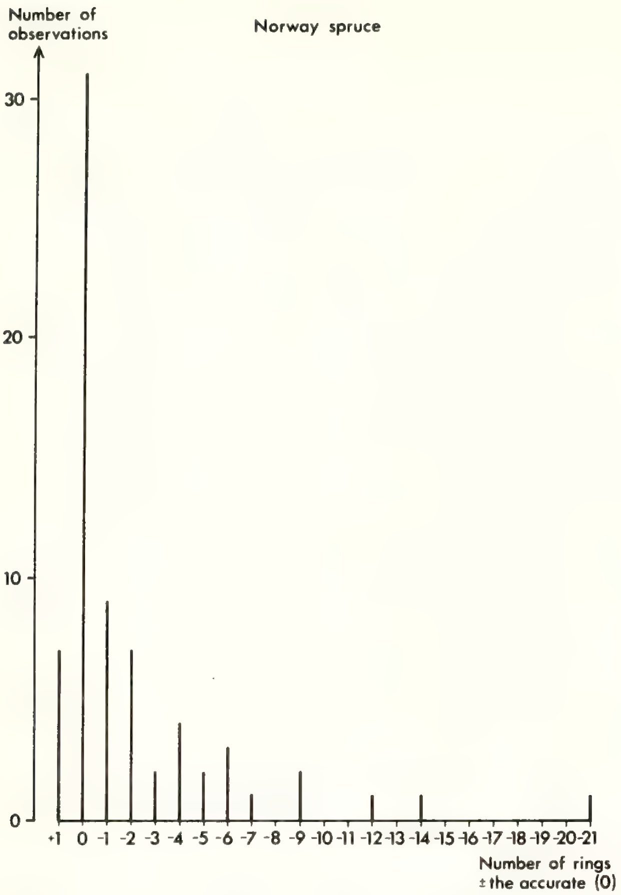


Figure 6.--The results of ring counts made in 24 spruce trees (Picea abies) scarred by fire in 1831. One cross section was taken out at the base of each tree, and ring counts were made in three directions in the wood formed after the fire (compare fig. 5). A total of 72 counts were made. The different numbers of rings found in the 72 observations are plotted in the figure.

(Fritts 1976), but in a specific case it could be very difficult to identify such a ring, especially if only a bore core is available. Taking into account all the problems involved in taking a core exact to the margin of the scar, it seems highly recommendable to use destructive sampling techniques when a more exact dating is needed. If cross sections are taken from a lot of spruces and at different levels of the stems, error could probably be minimized.

More severe dating problems arose when birch (Betula pubescens and B. verrucosa) from the same area described above was sectioned for dating purposes. Fullgrown trees of both the birch species often survive light surface fires and well-defined fire scars are formed. This was the case in the burned area from 1831. Because of a serious problem with decay, only 6 birches with fire scars could be used, and in one cross section, counts

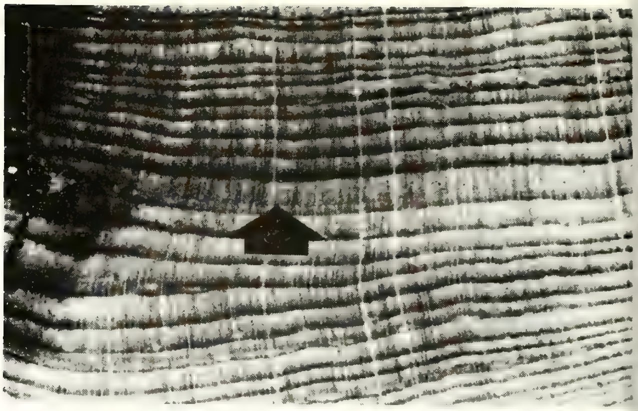


Figure 7.--A false ring formed close to the fire scar margin to the right. In a cross section of the scarred area it is rather easy to identi fy this type of false ring. If only a bore core is used, false rings can be a problem.

could only be done in two directions. As shown i fig. 8, no dating by counting rings in the healed-over wood gave the accurate date of the fire in 18 In one case, no less than 36 (25%) rings were missing. Despite the lack of sample material, the results at least indicate that the problems of datin fires by using birch could be more severe than expected.

Rings in the birch species (B. pubescens an B. verucosa) have often been used for calculating tree ages and reconstructing production capacities in birch stands (Fries 1964). However, the problem with absent rings has never been studied closely, but is sometimes mentioned as a possible error (Elkington & Jones 1974). To use birch for exact dating of fires seems rather hazardous without using a cross-dating technique, at least when very old trees are used as in this case. Between 253 and 369 rings were found at root neck level ir the birch trees investigated, which indicates rather high actual ages for all of the stems. Some of the trees are probably around 400 years old.

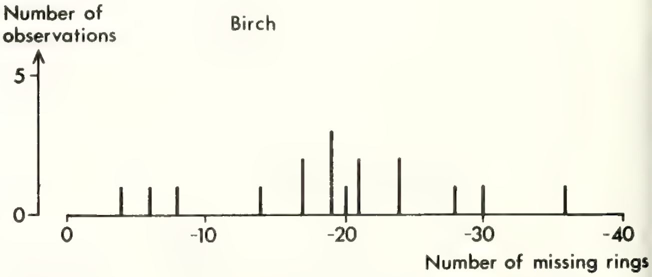


Figure 8.--The results of ring counts made on birch (Betula pubescens and B. verrucosa) scarred by fire in 1831. Ring counts were made in cross sections from 6 birches. In each cross section, ring counts were made in three directions in the wood formed after the fire. The number of missing rings in each ring count (observation) is plotted.

It is plausible that the difficulty with absent
igs is closely connected with high ages, and that
problem of getting accurate dates by ring
unts increases with the age of the tree. As
inted out by Kullman (1979), the problem of dat-
g young stems of Betula pubescens by ring counts
probably very small. The impression received
rough previous investigations made by the author
that younger trees are more useful for dating
es. However, an error of ±1 year seems to be
rd to avoid because of the special difficulties
und in birch in determining whether the scar
s produced late one growing season or early the
xt. This is a less severe problem in Scots pine
Norway spruce, where other wood structures
uld be used to specify the fire season.

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Fire History at the Treeline in Northern Quebec: A Paleoclimatic Tool[1]

Serge Payette[2]

Abstract.--The long term fire history at the treeline in Northern Quebec can be evaluated by ecological surveys of the major ecosystems. Available data suggest that fires are presently climate-controlled, and therefore may be used as paleoclimatic indicators. During a cold climatic interval, postfire tree regeneration is hindered, and a shift from forest to barren conditions is recorded. Examples from specific environments are provided in order to reconstruct significant ecological periods of the fire history since 3,000 years B.P. (Before Present). A preliminary interpretation indicates that these periods of climatic cooling are centered around 2,800-2,500, 2,200-2,000, 1,600-1,400, 1,100-900, 700 ?, 500-100 years B.P. and Present.

INTRODUCTION

The northernmost part of the boreal forest, called the forest-tundra ecotone, is particularly influenced by natural perturbations such as fires. Although of lower occurrence than in the boreal forest proper, fire has always been reported in the forest-tundra of Northern Quebec (Hare 1969; Rousseau 1968; Low 1896; Hustich 1939, 1951; Payette 1976), and is far more frequent than in the shrub tundra, either in Arctic Quebec or elsewhere in the Arctic (Wein 1976). Fire occurrence seems to be related to the importance of shrub and forest covers, which are closely dependent on the cool subarctic or hemi-arctic climate. Fires are climate-controlled under certain conditions, i.e., when weather initiates lightning, and when fuel is especially available through biomass production. Additionally, postfire tree regeneration is strongly influenced by climatic conditions prevailing during fire periods. Thus, fires may serve as climatic indicators of present and past ecological conditions of the forest-tundra. Reconstitution of the fire history in an area of adverse climatic conditions might help to detect paleoclimatic fluctuations, major changes of the forest cover, and, ultimately, any relative displacement of the treeline. The purpose of the present paper is thus to stress the importance, on a space-time basis, of forest-tundra fires in Northern Quebec, and to emphasize their paleoclimatic significance in ecological studies.

FIRES IN FLUCTUATING ENVIRONMENTS

A great diversity of habitats characterizes the forest-tundra landscape. The northernmost forests are selectively located in valleys and depressions protected from cold winds, and where water is available from snowmelt. In upland locations, but also in many lowland sites, the forests are replaced by shrubby and lichenic vegetation, including shrubby tree species stands called krummholz. Black spruce (Picea mariana (Mill.) BSP) is the most common krummholz-forming species. Krummholz are also found in the southern shrub tundra (or Low Arctic) in depressions, on gentle slopes, and on low summits. A more detailed account of the vegetation pattern in both plant zones has been published elsewhere (Payette 1976). It is generally assumed that the classical vegetation pattern of the forest-tundra, the so-called forest-and-barren landscape, can be viewed as a response to a set of ecological gradients related to wind and snow conditions, and also to soil properties. In fact, these ecological conditions are also expressing an underlying general climatic control, restricting tree populations to specific and favourable sites. During a warm climatic interval, it is presumed that forest transgression would occur, whereas under adverse conditions the reverse situation would prevail. This is a very simple and quite general model of the evolution of the forest cover and the migration of the treeline in relation to Holocene climatic fluctuations. The reality is more complex, since forest cover changes derive also from conditions of plant succession, plant reproduction strategies, and also of er environmental variables, where the time-lag the vegetation response to climatic changes is rly known. On the other hand, treeline dis- cements do not appear to be a mere expression major forest cover changes observed in southern as, because they are not always geographically l ecologically linked. The shift from one getation type to another is more frequently ieved by a major perturbation of the environ- t. Forest-tundra fires therefore appear to be portant catalysts of ecological change operating rough time, under the control of fluctuating imate. The forest-tundra of Northern Quebec ght be defined as an assemblage of postfire ant communities where forest regeneration generally ried on a space-time basis. In other words, the rest-tundra appears to be a vegetation zone nposed of a fire ecological mosaic, where the tation period varies strongly between different osystems and geographic areas. It is worthwhile, this context, to study the fire history in stinct parts and habitats of the forest-tundra, ose makeup is tightly associated with Holocene imatic fluctuations.

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As pointed out by Wright and Heinselman (1973) d by Wein and Moore (1979), one can reconstruct e fire history of a particular region within the ort term by historical document analyses, fire- ar and tree population age studies. Many pub- shed works concern this time perspective, for ample, in mixed hardwood-coniferous forest gions (Heinselman 1973, Cwynar 1977), and in real forest and forest-tundra regions (Rowe et al. 74, 1975; Johnson and Rowe 1975; Zackrisson 1977). second perspective emphasized by Wright and inselman (1973) and by Wein and Moore (1979) is lated to the long term environmental history, as vealed by pollen analysis (Swain 1973, Terasmae d Weeks 1979, Cwynar 1978) and where fire occur- nce is traced back to early Holocene forest bio- imates. In the forest-tundra and in the shrub ndra, the long term fire history can also be hieved by another approach related to ecological rveys based on soil-plant investigations of the jor ecosystems.

Paleoecological studies were conducted north d south of the modern treeline in Keewatin orthwest Territories) by Bryson et al. (1965), chols (1967, 1975) and Sorenson et al. (1971); ssil charcoals were found in paleosols, radio- rbon dated, and assigned to previous displacements the treeline. In Northern Quebec, studies on eeline dynamics related to paleoecological con- tions have been undertaken recently (Payette and gnon 1979), and research is focused on the evolu- on of terrestrial and peatland systems, where re is most influential.

One of the main hypotheses that underlies ese studies is that major periods of fire are limate-controlled, and depending on their occur- ence during warm or cold climatic intervals, act electively on tree or forest regeneration. There- ore any charcoal layer found in presently non- ooded sites is thought to represent the onset of a cold climatic period; as it was pointed out (Payette and Gagnon 1979), the paleoclimatic significance of the charcoal layer is strengthened if it belongs to a previous forest burn, but to a less extent if it is related to a black spruce krummholz burn. Identification of charcoal remains is necessary to prevent any misinterpretation, and, for example, the presence of charred cones of tamarack (*Larix laricina* (DuRoi) K. Koch) in the charcoal layer suggests more strongly that it is in fact a forest burn, since this species does not produce numerous and extensive eroded growth-forms like krummholz. We will briefly outline fire influence in the long term with examples from specific habitats whose development is thought to be primarily controlled by the present climate: the forest-and-barren system, the snowpatch system, the peatland system, and the sand dune system.

The Forest-and-Barren System

Virtually all forest and krummholz stands in Northern Quebec are of postfire origin. Forest fires in presently wooded stands are generally younger than 300 years old, and range between 50 and 250 years old. The oldest forest fires yet recorded in the forest-tundra by ^{14}C dating and age structure studies are about 450-500 years old in the white spruce (*Picea glauca* (Moench) Voss) fog belt along the Hudson Bay coast, and it is highly probable that older white spruce stands might be eventually found. Very small tamarack groves 400-500 years old have also been located in continental Northern Quebec (Payette and Gagnon 1979) and some of them appear to be older (Godmaire in prep.). As a general rule, charcoals found in forested soils of the forest-tundra are younger than 500-600 ^{14}C years B.P.

The fire history is quite different in krummholz stands of the forest-tundra and the shrub tundra. It is important to distinguish the *Cladonia*-krummholz sites of the southern forest-tundra from those of the northern forest-tundra and the southern shrub tundra. In the southern forest-tundra, fire frequency in *Cladonia*-krummholz stands seems to be related more or less closely to the fire frequency in forest stands found nearby. These krummholz are characterized by scattered eroded black spruces established from seeds. Their age may range from 10 to 250 years old. The wide occurrence of *Cladonia*-krummholz sites suggests that wildfires, since the onset of the Little Ice Age, are restricting forest regeneration to the most favourable habitats, and therefore causing a shift in the forest-barren cover ratio. The present landscape of the southern forest-tundra, with rather disjunct forests and widely distributed *Cladonia*-isolated black spruce trees, and *Cladonia*-krummholz stands, is a response to fire influence prevailing during a cold interval.

The extent of the *Cladonia*-krummholz habitat increases significantly in the northern forest-tundra and in the southern shrub tundra. Those located around tree groves are more or less closely linked to their fire history. In areas of large krummholz cover, the forest cover is highly disjunct or absent. In many regions of the modern treeline in continental Northern Quebec, Cladonia-krummholz stands are characterized by scattered black spruces; this vegetation type seems to be related to fires less than 500-600 ^{14}C years old. In Cladonia-dense krummholz sites, fire dates are generally older, up to 1,500-1,600 years B.P. according to the available data, suggesting a rather long fire rotation period. This situation does not seem unique, since it was observed through a wide area around the treeline in continental Northern Quebec (fig. 1). The main conclusion is that fire conditions are less frequently met in these sites because of adverse climate and, therefore, of low biomass production since the last fir period that occurred apparently during the second or later part of the Holocene climatic optimum (in the sense of Nichols 1976). In other words, since 1,600-1,500 years B.P. in some sites, and 1,100-1,000 years B.P. in others, fire frequency decreas because of climatic cooling. Regression of tree populations near the treeline in Leaf River area (58°15'N, 72'W) occurred also after these periods (fig. 1).

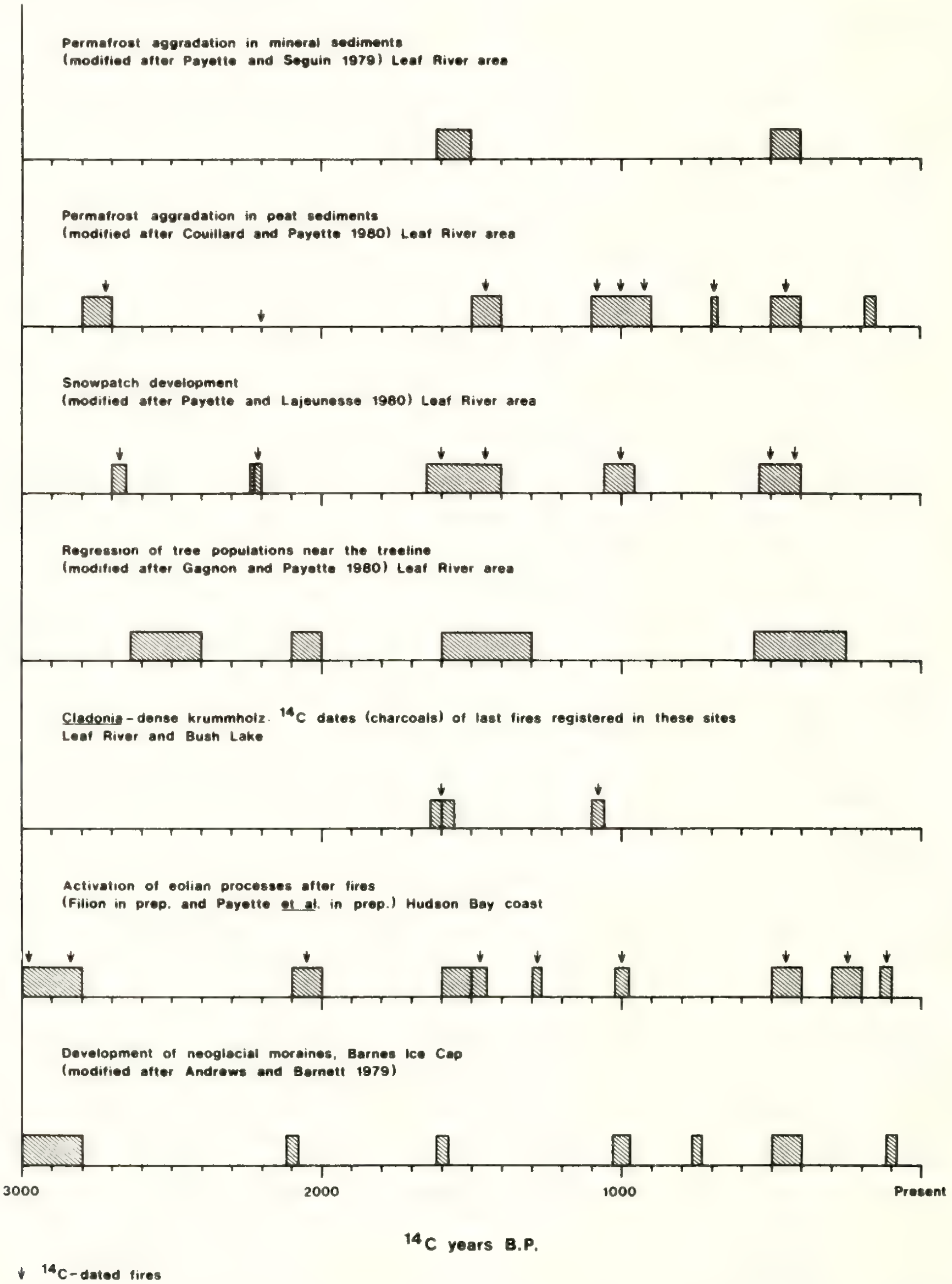

FIGURE 1: Preliminary correlation of fire chronology at the treeline in relation to Holocene climatic fluctuations in Northern Quebec (from 3000 years B.P. to Present).

The Snowpatch System

This system is widely distributed in the orest-tundra and in the shrub tundra. In a recent tudy, Payette and Lajeunesse (1980) showed that nowpatches near the treeline in continental orthern Quebec were previously forested. Their ocation in depressions near forest stands favors now accumulation, and the short growing season revents tree establishment. The nivation processes n this environment are producing geliturbation nd geliflucion of the solum, and buried soils re generally observed. The paleosols found in hese sites contain charcoals (including black pruce and tamarack cones) and wood fragments. adiocarbon-dated charcoals suggest that snowatches were formed after forest fires, when tree egeneration was hindered by cold climatic conditions around 2,600, 2,200, 1,600-1,400, 1,000-900 nd 500-300 years B.P. Fires were acting as atalysts in the deteriorating neoglacial climate fig. 1).

The Peatland System

Charcoals are commonly found in northern peatands, often in ombrotrophic peat formed during a limatic cooling. In minerotrophic or fen peatands, charcoals are also observed, although the rainage conditions are poor and woody vegetation enerally scarce. Under climatic cooling, permarost aggrades in the form of palsas and peat lateaus. The peat upheaving under permafrost rowth gives way to ombrotrophication and relative rying of the organic material. Forest and/or rummholz establishment follows this environmental hange, and is observed in the peat profile by harcoal layers located above the fen peat. ouillard and Payette (1980) have provided a eries of ^{14}C dates from charcoal samples collected n peat plateaus of the Leaf River area. The egistered fire periods match closely those obtained rom the snowpatch system, and are correlated with ermafrost aggradation since 2,600-2,700 years B.P., nder climatic cooling (fig. 1).

The Dune System

Dune landforms are widely distributed along he Hudson Bay coast both in the forest-tundra and n the shrub tundra. They are more scattered inand, where sand deposits are less extensive. ilion (in prep.) has sampled buried soils in dune ediments and observed that most of the time eolian rocesses were initiated by fires. In the northernost sites, she observed between 4 and 6 buried oils with charcoal layers containing small woody ragments; in southern sites, the number of charcoal ayers may be up to 9, and even 16 in one particular ite. The dune inception and further evolution are losely related to delay in forest and/or shrub egeneration after fire. Available data indicate hat fires dated around 3,000-2,800, 2,000, 1,400, 1,000, 450-250 and present were characterized by ctive sand deflation and sand accumulation processes across the forest-tundra of Northern Quebec (fig. 1). Present knowledge suggests that dune activity began at least 3,000 years ago; similar trends were observed in the Northwest Territories (west of Hudson Bay) since 3,500 years B.P. by Sorenson et al. (1971) and Sorenson (1977). Buried charcoal layers may yield a complete fire history of unstable xeric environments during cold intervals in different bioclimatic zones; thus specific fire frequency can be evaluated within the paleoclimatic framework.

DISCUSSION

Although palynology is providing an interesting format for the long term fire history reconstruction, ecological surveys may be also useful in seeking significant fire periods of the Holocene climates, which have caused important shifts in the vegetation landscape of both the forest-tundra and the shrub tundra. In order to evaluate the paleoclimatic significance of fires near the treeline in Northern Quebec, fire data gathered from different ecosystems are compared in figure 1; independent glacial events reported by Andrews and Barnett (1979) from the Barnes Ice Cap (Baffin Island), many hundreds of kilometers north of Northern Quebec, are compared to the fire chronology. The overall conclusion is that Holocene fire chronology is detectable in the ecological record, mainly during cold climatic intervals; the fire periods are synchronous between specific ecosystems, but also with neoglacial moraine development. At least for the past 3,000 years, important reduction of the forest cover occurred in the forest-tundra, due to direct influence of wildfires during cold intervals. At the present time, it is difficult to state whether the treeline regressed or not. For example, the 1,600-1,500 and 1,100-1,000 ^{14}C year-old burns found in Cladonia-dense krummholz sites of the shrub tundra cannot be assigned precisely to a forest or a krummholz fire. More data on plant macrofossil identification are needed to reach a firm conclusion. Nevertheless, it is possible that these fire periods correspond to different forest burns, and therefore to former forest or treeline positions north of the modern limits; the climatic cooling after these events did not provide opportunities for forest reconstruction; the Cladonia-dense krummholz appears to be a rather stable ecosystem, operating over many centuries. Clearly, these stands would become extinct if fires were ignited in the near future. On the other hand, charcoals found in non-forested habitats, as in the snowpatch environment, does not prove that the treeline has regressed; it points out that the forest cover retracted during the Neoglacial. The same interpretation must be held for fossil charcoals found in any periglacial landform of the forest-tundra, as in polygonal-patterned grounds south of the modern treeline. These events may not always be evidence of treeline displacements, as suggested by Sorenson et al. (1971) and Sorenson (1977); for instance, periglacial landforms are presently produced far south of the forest border in open sites and also under tree covers; but they indicate at least the incidence of a cold period, and a subsequent regression of the forest cover. Evidence of treeline migrations based on macrofossil studies of timber has been demonstrated mainly in mountain ranges (LaMarche 1973, Denton and Karlén 1977, Kullmann 1979), and only at a few locations in high latitude regions (Ritchie and Hare 1971). Buried soils with charcoals (without confirmation of tree growth-forms) in tundra regions suggest the presence of former woody vegetation, but not necessarily forest vegetation. So, the ultimate evidence of northward treeline migrations in the Arctic is obtained from fossil tree stems and other plant remains that belong to tree growth-forms. Such a proof has been recently presented by Gagnon and Payette (1980) from Arctic Quebec; a buried tamarack forest made of several well-formed stems has been discovered in a fen peatland, about 10 kilometers north of the modern forest line; this paleoforest is about 2,800 ^{14}C years old and represents, at the present time, the unique evidence of Holocene forest line fluctuations in Northern Quebec.

Fire occurrence in tundra and in forest-tundra of northern North America has been more or less used to reconstruct Holocene paleoclimates (Bryson et al. 1965, Sorenson et al. 1971, Nichols 1975, Payette and Gagnon 1979, Gagnon and Payette 1980). Because of its critical position in northern lands, the forest-tundra ecotone is highly sensitive to climatic fluctuations. In this connection, wildfires of the present and the past provide a rather complete record of significant events that have affected the major ecosystems. Fire history in presently forested lands of the forest-tundra can be obtained by classical methods including fire scar and tree population age studies; this cannot be the case for non-forested lands, although geographically and ecologically linked to the forest dynamics. Ecological surveys based on soil-plant relationships of the major ecosystems of the forest-tundra and the shrub tundra, supplemented by the space-time framework, appear to be a useful approach in the reconstruction of fire history, or more precisely, in the reconstruction of significant ecological periods of the fire history, revealing the overwhelming influence of Holocene climates. A preliminary interpretation of all available data suggests that cold intervals of the last 3,000 years appeared around 2,800-2,500, 2,200-2,000, 1,600-1,400, 1,100-900, 700 ?, 500-100 years B.P., and present.

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Bibliography of Fire History: A Supplement[1]

Martin E. Alexander[2]

INTRODUCTION

A bibliography on forest and rangeland fire history containing 307 references was completed during the winter of 1979 and released in the spring of 1980 (Alexander 1979). Nearly five hundred copies have been issued to date. I have casually kept track of new and overlooked literature since publication and included 26 additional references (numbered 308 to 333) here. The citation form and abbreviations used in the original document have been retained for continuity. Subject and area indexes consistent with those of the published bibliography, are provided for user convenience. Worth noting is the excellent review published recently (Maeglin 1979) on the methods, care, and use of increment borers. A number of minor errors in the original printing have been discovered and a list of the relevant corrections is provided here for completeness. This supplement has been prepared and included in these proceedings for the benefit of workshop participants and others interested in keeping abreast of available fire history information.

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CORRIGENDA

Acknowledgments page, line 4: insert Gerald F. Tande after Frederick J. Swanson.

Table of Contents page, Cover photographs, line 7: should read "...page 13G"

Page 13, Reference #9: add "[French version also available as: Deux siècles et demi de feux de forêts enregistres]" at the end.

Page 15, Reference #34: should read "Historic fires in the..." and 130 p. instead of 128 p.

Page 17, Reference #47: should be 1975 rather than 1976.

Page 17, Reference #56: should read "Chimney Spring forest fire history."

Page 23, Reference #124: should read "...interpreted mainly using pollen..."

Page 30, Reference #200: should read "Plummer, F.G."

Page 31, Reference #211: should be 152 p. instead of 179 p.

Page 33, Reference #231: citation should read Singh, G., Kershaw, A.P., and Clark, R. 1980. Quaternary vegetational and fire history in Australia *in* Fire in the Australia Biota. Australian Acad. Sci., Canberra, A.C.T. [in press].

Page 34, Reference 246: citation should read Interl. Palynological Conf. (June 29-July 6, Cambridge, England) Abstrs. 5: 381.

Page 35, Reference #261: should be 1980 rather than 1979.

Page 39, Reference #304: paper will not be published.

Page 39, Reference #305: should be 1979b rather than 1980 and note volume 10.

Page 41, Table 2, #1: Expected completion date should read June 1980.

Page 42, Table 2, #14: should be Stephen [instead of Steven] W.J. Dominy.

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Fire History Terminology: Report of the Ad Hoc Committee[2]

William Romme, Committee Chairman

It is often quite difficult to compare fire istory studies conducted by different investigaors because different terms may be used to refer the same concept and the same term may be used refer to different concepts. To help resolve is difficulty, an ad hoc committee was formed arly in the course of the workshop with the task f (1) listing the most confusing terms commonly sed in fire history studies, (2) determining hich terms are actually synonymous, (3) suggestng which of several synonyms is the best term to se in future fire history studies, and (4) proiding a definition for each of the preferred erms. The committee was composed of Martin lexander, Stephen Arno, Kathleen Davis, H. William abriel, Edward Johnson, Michael Madany, William omme, Gerald Tande, and Dale Taylor. The commitee presented its preliminary report to all of the orkshop participants during the concluding session, nd a concensus was reached on the meaning and preerred use of several terms. Copies of the preiminary report were also distributed to several ther fire history researchers who could not attend he workshop. Following a 3-week period during hich several people made additional comments, this inal version of the committee's report was written y William Romme. This is not meant to be an exaustive fire history glossary nor a complete docuentation of definitions as used in the literature. ather it focuses on those terms that caused the reatest confusion at this workshop and are in reatest need of clarification. The individual apers in these proceedings do not necessarily use he terminology recommended in this report, as they ere prepared before the committee was formed. Howver, it is hoped that the recommendations below ill help to improve communication in future papers ealing with fire history.

We must add that although terminology can be serious source of confusion, another major probem in comparing fire histories is related to diferences in the size of our study areas. Concepts ike fire frequency and mean fire interval take on ery different meanings when applied to a 0.1-ha tand as opposed to a 100,000-ha park. We emphaize the importance of clearly stating the size of he area referred to by these terms. But there are till problems in comparison even if the sizes of he study areas are specified, especially when two tudy areas differ markedly in size. It may not e appropriate to extrapolate findings based on a mall study area to a larger area, or vice versa. Not only are there probably differences in sampling intensity in large and small study areas, but extrapolation by simple multiplication or division may be quite misleading. For example, if there were 10 fires in a particular area during some time period of interest, it does not necessarily follow that there were 100 fires in an area 10 times as large. Similarly, if 10% of a 100,000-ha park burns each year, it is not necessarily true that 10% of every 0.1-ha stand burns each year. At this time, we can offer no solutions to these problems of study area size; we simply remind investigators of the problems, and urge caution in making comparisons or extrapolating results. Hopefully some future fire history workshop can resolve this difficulty.

The following terms are those for which a concensus was reached by the participants at the workshop. The preferred terms are given first, with other synonyms (if any) in parentheses:

1. FIRE OCCURRENCE (or FIRE INCIDENCE) = one fire event taking place within a designated area during a designated time (no units; either yes, a fire occurs, or no, a fire does not occur).

   COMMENTS:

   (1) These terms have sometimes been used to refer to fire frequency (as defined below) with specific reference to some large study area, as opposed to fire frequency at a single point. This use is semantically inaccurate, however, as "occurrence" or "incidence" implies one event. Therefore, we recommend the term fire frequency (see below) for this meaning.

   (2) Neither synonym is clearly superior to the other, but only one term is needed. We recommend the term fire occurrence.

2. FIRE INTERVAL (or FIRE FREE INTERVAL or FIRE RETURN INTERVAL) = the number of years between two successive fires documented in a designated area (i.e., the interval between two successive fire occurrences); the size of the area must be clearly specified (units--years).

   COMMENTS:

   (1) These terms have been used to indicate mean fire interval, etc. (see below), but we should distinguish between individual fire intervals and mean fire intervals.

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[1] A product of the Fire History Workshop, Laboratory of Tree-Ring Research, University of Arizona, Tucson, October 20-24, 1980.

(2) None of these three synonyms is clearly superior to the others, but only one term is needed. For the sake of brevity, we recommend the term fire interval.

(3) Writers should indicate whether a reported fire interval has been corrected by cross-dating the individual fire occurrences (see below).

3. MEAN FIRE INTERVAL (or MEAN FIRE FREE INTERVAL or MEAN FIRE RETURN INTERVAL) = arithmetic average of all fire intervals determined in a designated area during a designated time period; the size of the area and the time period must be specified (units --years).

COMMENTS:

(1) None of these three synonyms is clearly superior to the others, but only one is needed. To be consistent with the term fire interval, recommended above, we recommend the term mean fire interval.

(2) The frequency of distribution of fire intervals also should be examined. With highly skewed distributions, for example, the median fire interval or some other statistic may be more meaningful ecologically than the mean.

(3) Hypothetical Example--"Fire occurrences in the years 1750, 1800, and 1900 were documented in a 10-ha study area, based on fire scar analysis corrected by cross-dating. Fire intervals of 50 and 100 years, respectively, were thus determined. Therefore, the mean fire interval in a 10-ha stand between 1750 and 1900 was 75 years."

Note that these fires may or may not have burned the entire 10-ha stand. All we know for certain is that 3 fires occurred somewhere within the stand during a 150-year period, and the average interval between successive fires in the stand was 75 years.

4. FIRE FREQUENCY = the number of fires per unit time in some designated area (which may be as small as a single point); the size of the area must be specified (units--number/time/area).

COMMENTS:

(1) This term has been used in a more restrictive sense to indicate that the area referred to is a single point or a very small stand, while some other term (e.g., fire incidence or fire occurrence) is used in reference to a larger area. However, we recommend using only the term fire frequency for areas of all sizes (with the size of the area clearly specified) because (i) if two different terms are used, it may not be clear which is appropriate in study areas of borderline size, i.e., bigger than a point but smaller than a large area; (ii) there is no semantic reason why the term frequency must be restricted to an area of any particular size; and (iii) it is semantically inaccurate to use terms like occurrence and incidence to refer to multiple events, as noted above.

(2) Hypothetical example: "Intensive fire-scar sampling, corrected by cross-dating produced evidence of 100 fire occurrence during the last 50 years in a 10,000-ha National Park. At one point within the Park (i.e., a single fire-scarred tree) there was evidence of 10 fires during th same 50-year period. Therefore, the fir frequency during the last 50 years in a 10,000-ha study area was 100 fires/50 ye 10,000 ha, or an average of 2 fires/year 10,000 ha. The fire frequency at a sing point during the same time period was 10 fires/50 years/point, or an average o 0.2 fire/year at a point, or 1 fire/5 ye at a point."

(3) Fire frequency in a large area indicates only the number of ignitions in that are during some time period; it reveals noth about the sizes of the fires or their ecological effects. When referring to a large area, therefore, the amount of area burned per unit time may be more meaningful than simply the number of ignitions per unit time. With very smal areas or single points, however, the number of fires per unit time is useful information.

5. CROSS-DATING = correcting the chronology dete mined from an individual tree-ring sample by comparison with a master tree-ring chronology developed for the area (no units).

COMMENTS:

(1) This term has been used to refer to the process of correcting fire dates in a master fire chronology by adjusting individual sample dates to correspond tc dates obtained from nearby fire-scarred trees. However, the term should not be used except in reference to a master tree-ring chronology for the area.

(2) When reporting fire dates determined by dendrochronological methods, it is important to distinguish between fire date that have been corrected by cross-dating and fire dates that have been estimated without cross-dating.

MASTER FIRE CHRONOLOGY (or COMPOSITE FIRE INTERVAL) = a chronological listing of the dates of fires documented in a designated area, the dates being corrected by cross-dating (defined above); this master fire chronology is compiled from several individual fire chronology sources (e.g., individual trees, stumps, stands, or written fire records), and is then used to determine fire frequency, mean fire interval, and other fire history parameters; the size of the area must be clearly specified (no units).

COMMENTS:

(1) Neither synonym is clearly superior to the other, but only one is needed. We recommend the term master fire chronology.

(2) If a master fire chronology is constructed without correction of individual fire dates by cross-dating, this should be clearly indicated by calling it an "un-cross-dated master fire chronology" or some similar term.

(3) Many of the master fire chronologies previously reported in the literature have not been corrected by cross-dating.

FIRE SENSITIVE TREE = a species with thin bark or highly flammable foliage that has a relatively greater probability of being killed or scarred by a fire (no units). A FIRE RESISTANT TREE is a species with compact, resin-free, thick corky bark and less flammable foliage that has a relatively lower probability of being killed or scarred by a fire.

FIRE SCAR SUSCEPTIBLE TREE = a tree of any species that has already been scarred by fire at least once and has a relatively greater probability of being scarred by the next fire (no units).

COMMENTS: The term fire susceptible tree has been used to express this meaning, but for clarity the tree should be referred to as fire scar susceptible.

STAND-REPLACING FIRE (or STAND-RENEWING FIRE or STAND-DESTROYING FIRE or STAND-REGENERATING FIRE) = a fire which kills all or most of the living overstory trees in a forest and initiates forest succession or regrowth (no units).

COMMENTS: None of these four synonyms is clearly superior to the others, but only one is needed. We recommend the more neutral term stand-replacing fire.

The following terms were also discussed at the workshop, but no concensus was reached regarding their precise meanings or the preferred synonyms. They are useful terms, but because they may be used in different ways by different investigators, each writer should clearly specify his/her intended meaning.

A. FIRE CYCLE or FIRE ROTATION = the length of time necessary for an area equal to the entire area of interest to burn; the size of the area of interest must be clearly specified (units--years/area).

COMMENTS:

(1) These terms have sometimes been used with reference only to stand-replacing fires. However, there is no semantic reason why the terms could not be used with reference to non-stand-replacing fires as well.

(2) Note that the entire area of interest need not necessarily burn; some portions may burn more than once while other portions do not burn at all, as long as the sum of hectares burned by each individual fire equals the total number of hectares in the area of interest.

(3) This concept has sometimes been referred to as the natural fire rotation. In these cases the intended meaning of the word "natural" should also be defined.

(4) This is a useful concept, and one synonym or the other should be adopted for general use. However, participants at the workshop expressed strong preferences for both terms, and no concensus could be reached.

B. FIRE INTENSITY and FIRE SEVERITY. There was considerable disagreement about the meanings and uses of these terms, which probably are not synonymous. Some argued that fire intensity should be used only in a strict thermodynamic sense (i.e., units of energy released/area or length of fireline/time), while fire severity should be used to indicate the effects of a fire on the ecosystem (e.g., changes in the forest floor, the canopy, the total photosynthetic area, etc.). Others argued that in fact we rarely can measure the actual energy release of a fire, but we can readily determine its relative intensity by examining its ecological effects. Thus, it is appropriate to call a stand-replacing fire a high intensity fire, and to call a fire that produces little mortality a low intensity fire, there being nothing to gain by introducing an additional term like fire severity. Writers should be careful to define these terms whenever using them.

C. FIRE PERIODICITY. This term is often used, but we could arrive at no concensus as to its meaning. It was difficult even to produce a tentative definition, so writers should be very explicit about what they mean by the term.

Workshop Summary: Who Cares About Fire History?[1]

Robert W. Mutch[2]

INTRODUCTION

Threads of continuity ran through this excellent workshop. The workshop was characterized by an abiding interest in a common terminology, concern about scale (how large, or small, an area can be represented), the resolution of data required to make effective management decisions, recognition of the limitations of fire history information, the cultural, biological and environmental stratification of data, and animated discussions regarding differing methodologies. These threads wove a unifying strength into the workshop's fabric. But some of the participants harbored reservations about the utility of fire history information; thus, the question: Who cares about fire history? This questioning remark was overheard during one of the informal discussion periods, and it is an appropriate one to ask.

APPARENT LIMITING FACTORS

Certain factors limit the interpretation and application of fire history information and pose potential reasons for not caring:

1. Flammable exotic species tend to obscure "natural" fire frequencies (e.g., Bromus rubescens in Sonoran Desert, Bromus tectorum in Great Basin, Melaleuca in Everglades).

2. Changing cultural activities over time confound the "natural" fire history record (e.g., burning by aboriginals, miners, trappers, settlers).

3. Climatic changes occur.

4. Grazing patterns change.

5. Fire scars represent a conservative history (fires must be intense enough to scar the cambium tissue).

6. Stratification of data is sometimes diff cult.

7. It is difficult to date events in certai ecosystems (for example, fires in the Sonoran Desert leave few direct signs).

8. Fire chronologies that are not cross-dat may impair the accuracy and amount of in formation collected.

9. The importance of fire history informati to fire suppression, prescribed fire, an land management planning programs is not fully recognized.

For these reasons, and possibly others, it would be easy to discount the importance of fire history studies. Despite these limitations, workshop participants did care about fire history info mation and its application to management programs Fire history results were reported from northern Quebec to the Northwest Territories, New England and Florida to Oregon and California, and from Sweden and Australia.

FIRE HISTORY METHODOLOGIES

Many methods were presented to determine the fire history of a point or area, including the direct dating of fire scars in the annual rings of trees and numerous indirect procedures. Direct dating techniques essentially followed the cross-dating methods developed by the Laboratory of Tree Ring Research, University of Arizona, or utilized an alternative method as described by Steve Arno and Kathy Davis. Lake sediment analyses for polle and charcoal provided additional direct, but less precise, estimates of fire intervals. Indirect methods for determining fire history analysis included land survey records, informants, journals, and fire occurrence records, inferences derived from the adaptive strategy of species, and age class distributions of fire originated stands.

QUESTIONS AND CONCEPTUAL CHALLENGES

Bill Moir questioned our ability to stratify fire history information in meaningful ways, demor strating that if you've seen one canyon woodland you haven't necessarily seen them all. The issue f stratification came up repeatedly during the workshop. Investigators subdivided time and space in terms of prehistoric and historic periods, environmental gradients, and plant communities. Fire history information obviously will be more readily extended and applied to resource management programs, if it can be organized according to recognized classification systems. For example, the interpretation of fire history data in different environments (through habitat types) has facilitated management applications in the northern Rocky Mountains.

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[1] Prepared for the Fire History Workshop, Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, October 20-24, 1980.

[2] Fire Management Officer, Lolo National Forest, Missoula, Montana.

Fire history and fire ecology relationships in the east and northeast often have not been addressed with the detail devoted to our understanding of western ecosystems. It was encouraging to see Craig Lorimer and Serge Payette apply land survey records and paleoecological methods to further the understanding of fire in eastern ecosystems. Lorimer's results suggested a 400- to 800-year fire interval in his study area in the northeast. Because such an event is infrequent, does this imply that the effect of that event is insignificant? Fred Hall tended to contrast understory burning vs. crown fire regimes in a competitive sense, indicating that understory burning is more important than crown fires. Is it appropriate to consider one type of fire regime as being more significant than another type? Or should we recognize that different plant communities are regulated by different intervals, types, and intensities of fires? Thus, infrequent crown fires are as normal to lodgepole pine forests as frequent surface fires are to ponderosa pine forests.

Is it possible to discuss fire history results in an objective manner? Words like degradation, disastrous, and damage crept into some of the discussions during the week. Can our interpretations of fire history be unbiased if we employ such value judgments in our assessment of fire intervals and their effects on ecosystems? Shouldn't resource management objectives provide the criteria for determining whether a given fire is beneficial or harmful?

Several investigators appreciated that tree rings portrayed only a narrow slice out of the time sequence of a region's fire history. Examples of paleoecological research were presented that dramatically extended fire history information back to prehistoric periods. Gurdip Singh presented some tantalizing results regarding the pollen and charcoal record in southeastern Australia. Results such as these should provide us with new insights regarding the evolutionary adaptedness of plant communities to varying fire intervals. And although we should never expect to acquire fire chronologies that rival the time span encompassed in Wes Ferguson's bristlecone work, more attention to crossdating would permit us to push fire history information further back in time.

Fire interval information, when coupled with the knowledge of a site's productivity, can be instrumental in evaluating the effects of attempted fire exclusion actions. The effects of 50 years of fire suppression will be more readily discernible in the Arizona ponderosa pine stands where fire intervals are around 2 years than in the cedar-hemlock stands of northern Idaho where the return interval can exceed 200 years. On the other hand, low productive sites characterized by warm-dry and cold-dry environments should not be as adversely affected by fire exclusion as moderately productive sites with frequent fire intervals. Thus, information about fire intervals and productivity is important to the resolution and scheduling of prescribed fire activities.

An assumption that stands are uniformly flammable over time does not fit all plant communities. Contrast the frequent, sometimes almost annual, fire intervals in ponderosa pine with the more infrequent intervals in lodgepole pine. And we must recognize, too, that there is considerable variation in fire intervals within each of these types with more frequent intervals in western Montana lodgepole pine as compared to the Yellowstone National Park lodgepole stands. We can use such fire history information to infer relationships about the presence or absence of fuel-free periods in these plant communities. Such fuel succession information is useful in defining opportunities for prescribed natural fire programs. If age class mosaics serve to regulate fire size, this knowledge provides a measure of confidence that Yellowstone National Park is large enough to contain fires freely burning under prescription. Conversely, if we are losing the expression of an age class mosaic as in the chaparral type of southern California, we can expect an increase in high intensity, large fires (as the 16- to 18-year fire interval is dampened by suppression efforts).

There may be a new opportunity for real-time fire history studies in the future, due to the natural laboratory provided by long duration (up to 5 months) prescribed fires in national parks and wildernesses. Tommorrow's fire historian has the chance to live with these fires on a day-to-day basis, observing which trees are scarred, when they're scarred, and how they're scarred; and also observing events that contribute to the nonscarring of trees. These observations, coupled with the distribution of fire intensity classes and stand mosaics associated with individual large fires, could improve our understanding of fire interactions with plant communities. Also, the seasonal collection and analysis of fire-scarred specimens on prescribed fires might permit us to determine the seasonality of historic fire occurrence, as well as the year of occurrence.

MANAGEMENT APPLICATIONS

The workshop described some land managers as not always being careful, unenlightened, victims of their own inadequate literature searches, and guilty of seemingly irrational suppression decisions in many instances. These perceptions of a manager need to be interpreted in terms of his environment:

1. Subject to endless deadlines.
2. Accountability for hard targets and planned accomplishments.

3. A daily schedule driven by phone calls and a steady stream of mail with due dates.

4. Often a crisis-oriented decisionmaking atmosphere.

5. Too little time to read and reflect.

6. A sincere desire to do better (which means applying our current knowledge base in the decision making process).

To the question, "Who cares about fire history?," many managers today would respond with an "I care!" Fire Management policies today are more closely aligned with the resource objectives of agencies like Parks Canada, National Park Service, Bureau of Land Management, and USDA Forest Service. As imprecise as fire history information may be, an increasing number of enlightened land managers consider it to be absolutely essential, not just "nice to know", data for land management planning purposes. Researchers and managers need to acquire the necessary patience and perseverance to work closely with each other. Just because a study is published and distributed to library and office shelves is no guarantee that the information will be applied. Effective application will be realized only when the researcher and manager agree to meet each other more than half way. In other words, each must have the desire to live a little in the other's world.

Some of the practical applications of fire history information as stated by Kathy Davis and others are:

1. A basis for silvicultural prescriptions.

2. A basis for fire behavior predictions on wildfires.

3. A data base for land management planning.

4. A scheduling guide for prescribed burning activities to simulate natural intervals (some warning signals to observe when we exclude fire for too long, or return it too frequently).

5. An aid in prescribed burning and prescribed natural fire planning (effects of past fire exclusion related to different fire intervals, public understanding of prehistoric and historic role of fire, potential fire intervals and fire sizes, etc.). Steve Barrett provided evidence to consider aboriginal burning as a measurable element in natural ecosystems.

6. An example to gain homeowner's attention to the fact that fires are inevitable in most plant communities. The fire history record indicates that although we may postpone fires we will not eliminate them from the urban/wildland interface.

7. A backdrop to guide development of post-fire rehabilitation programs. Fire history and fire effects information demonstrate that fire adapted plant communitie have evolved mechanisms to rehabilitate themselves; and that massive re-seeding programs often can be avoided.

SUMMARY

The purpose of the workshop was to exchange ir formation on sampling procedures, research methodol ogy, preparation and interpretation of specimen material, terminology, and the application and significance of findings. That Marv Stokes and Jack Dieterich were right on target in providing a productive forum for such discussions is best exemplified in the remarks of the participants themselves. Many felt that it was one of the most informative workshops they had ever attended. Those in attendance also agreed that the pace was quick, and that energy levels remained high. Challenging discussion punctuated the delivery of diverse and stimulating papers as people freely shared ideas with each other. And the warm hospitality of the faculty and staff of the Laboratory of Tree-Ring Researc provided a comfortable environment for communications.

One of the objectives of the workshop was to emphasize the relationship of dendrochronology procedures to fire history studies and interpretations. Although his outward demeanor was calm, Marv Stokes must have been inwardly wincing at the absence of cross-dating procedures in some of the tree-ring investigations. Lively debates ensued regarding the need for cross-dated chronologies in all cases. And Tom Harlan provided the group a moment's pause when he indicated that it could tak up to a year for a person to develop competency in dendrochronology procedures. Yet the participants went away with a better appreciation for the increased accuracy and information content that results when standard dendrochronology methods are followed. More than one individual indicated an interest in developing cross-dated chronologies in future studies.

Most tree-ring investigators stated that they were essentially forced to take material wherever they found it and were unable to follow a rigid sampling design. One saving point is that a few trees seem to capture most of a stand's fire history story. But there's probably a need to better involve biometricians to strengthen sampling procedures where possible.

A final footnote is in order--and that has to do with the warm kinship the workshop participants all felt towards Harold Weaver and his lovely wife Billie. Having this grand gentleman of ponderosa pine management with us all week added immeasurabl to the workshop's atmosphere. Thanks to both of you for joining with us and for giving us the opportunity to get to know you better.

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U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

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Bottineau, North Dakota
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Lubbock, Texas
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526

Tradeoff Analysis in Local Land Management Planning

Thomas C. Brown

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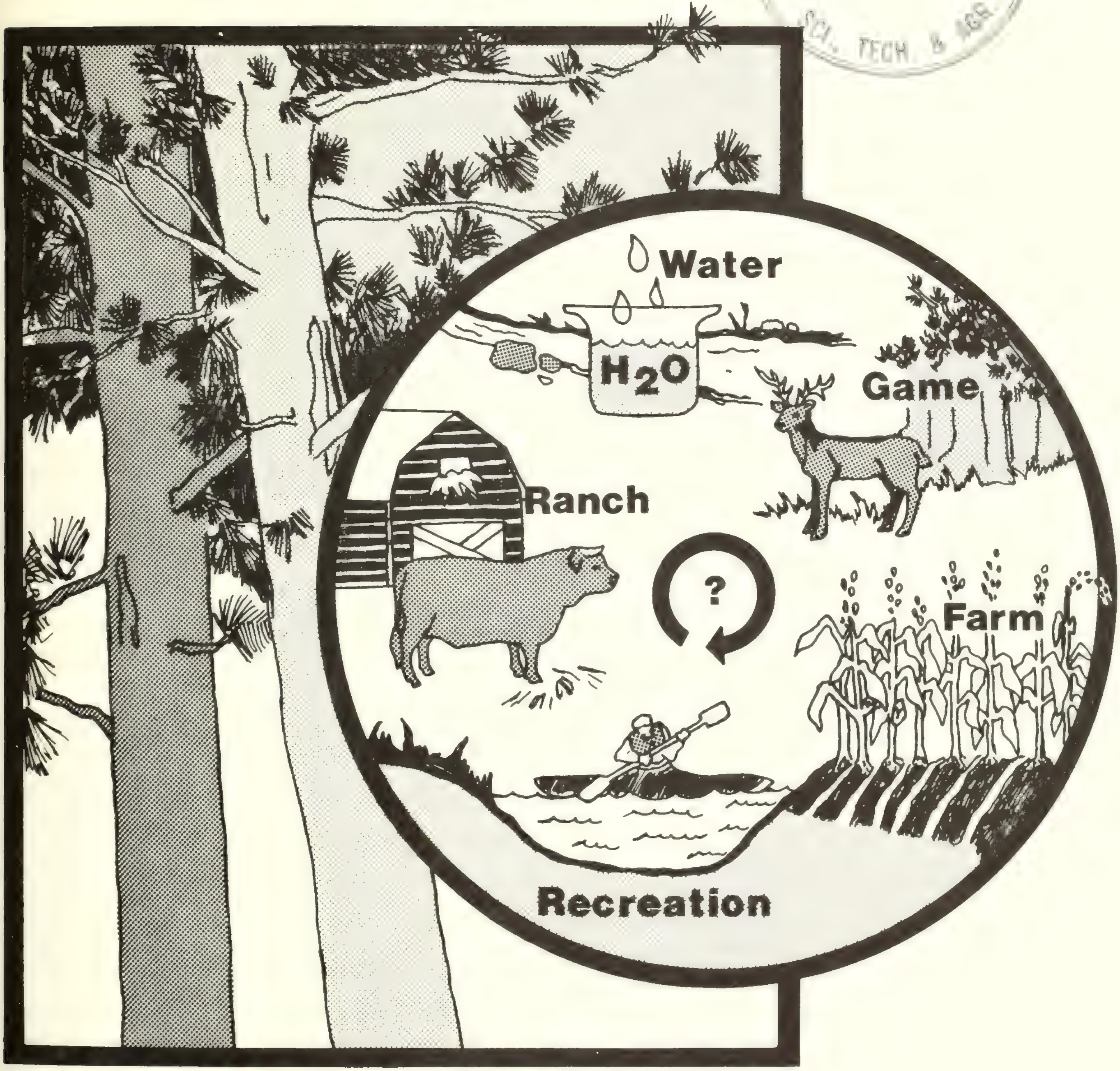

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U.S. Department of Agriculture

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Tradeoff Analysis in Local Land Management Planning

Thomas C. Brown, Economist
Rocky Mountain Forest and Range Experiment Station[1]

Abstract

A set of concepts, procedures, and displays is presented to facilitate land management planning at the local level. The emphasis is on tradeoffs (analysis) in the formulation of alternatives, the estimation of the effects of the alternatives, and the comparison of the alternatives.

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[1] Central headquarters is in Fort Collins, in cooperation with Colorado State University; research reported here was conducted at the Station's Research Work Unit at Flagstaff, in cooperation with Northern Arizona University.

Tradeoff Analysis in Local Land Management Planning

Thomas C. Brown

Introduction

This report is concerned with comprehensive land anagement planning at the local level, such as on a ational forest. The focus of the paper is on the /stematic consideration of tradeoffs between alter-atives for given resources. Within the context of an /erall planning process, four critical steps in the election and comparison of management alternatives re examined: (1) analysis of the management situa-on, (2) formulation of alternatives, (3) estimation the biophysical and socioeconomic effects of the ternatives, and (4) comparison of the alternatives. ther, equally important planning steps, such as ssessment of management concerns and public issues, nd selection of planning criteria, are not examined ere.

This report should help students, resource man-gers, and others particularly interested in local-level nd management planning to better understand the anning process. It provides persons involved in land anagement with an overview of critical steps of the cal-level planning process and displays to facilitate mpletion of those steps.

The Challenge—An Example

The following hypothetical situation is used to illus-ate the kinds of information needed to arrive at a anagement program that will provide a reasonable ix of goods and services, both commodity and amen-y, while preserving land productivity.

The "Ponderosa Forest," on public land, is the urce of a river that provides water for "Pineville," a ral community at the Forest edge, and "Metro City" me distance away. The river also provides irrigation ater for farmlands between the two communities.

The Forest is popular with recreationists from Metro ity, and more distant places, who hike, ski, camp, sh, hunt, ride off-road vehicles, and seek wilderness periences.

The Forest provides timber for wood products. awmills and other wood-related industries employ early 20% of the working force in Pineville.

Several family-run ranching operations near Ponder-a Forest depend on its grasslands for summer forage for their livestock. The livestock help meet the demand for beef.

The environment is diverse. Several types of soils are interspersed over the area. Shrublands and grasslands typify the lower elevations, forested slopes and meadows the middle elevations, and rocky outcrops the mountain tops. The higher elevations receive the most rain and snow.

A highway, several unpaved roads, and some off-road vehicle (ORV) and hiking trails traverse much of Ponderosa Forest, but one-quarter of the area is still roadless.

Demands for the resources from Ponderosa Forest are increasing rapidly. Some groups—even from out-of-state—want roadless areas designated as wilderness. Wood industries want timber harvested on additional areas to sustain jobs in Pineville and meet demands for wood products in Metro City and beyond. Off-road vehicle clubs want more areas designated for ORV use. Hikers want more trails closed to ORV's.

Farmers are asking for more irrigation water from streams and reservoirs. At the same time, fishermen want enough water in streams and reservoirs to safeguard fish habitats. Satisfying both would require heavy thinning of the forest to reduce water consumption by trees and thereby increase runoff.

Ranchers fear that added recreational activities will force their livestock from the range. Sportsmen want more of the range devoted to game animal habitat.

Completely satisfying all interests is impossible. A compromise lies somewhere between the diverse wants and the capacity to meet them.

Vital questions must be considered during the planning process. Where are the resources? What is their condition? How accessible are they? What are the opportunities to improve production of individual resources? How will changes in one resource affect others? Although it is not possible to answer all of the questions completely, the most current information and technology can help describe the complex interactions among the resources involved (fig. 1).

The large volume of information needed to answer such questions and the complexity of most biophysical and socioeconomic environments require a comprehensive, systematic, analytical, and interdisciplinary planning effort. To make the options understandable to decision makers and interested citizens, techniques must be used to select the most relevant information and effectively communicate that information.

The Response—Tradeoff Analysis

A plan is needed to direct future management, clearly describing any changes from recent management. Such a plan must recognize the contribution of the local area to regional and national goals, as well as to local interests. The plan should be a unique blend of efficiency and equity concerns.

One process for deciding how public land should be managed involves a focus on tradeoffs. A tradeoff is a relationship between two or more effects of a change in some condition (such as the condition of the forest). The relationship signifies a difference between the initial condition and the new one which the change would bring about. For example, a 50% increase, from the current condition of some portion of the Ponderosa Forest, in availability of snags for cavity nesting birds would cause a decrease in timber yield of 50 board feet per acre. The difference between the two conditions can be described in terms of the tradeoff between 50 board feet per acre and a 50% increase in the number of snags.

The advantage of examining tradeoffs between forest conditions is that attention is focused on actual quantities and values of those quantities rather than on abstract values. Abstract values, characterized by statements such as "timber is more important than range," generally are of little use in decision making because they do not apply to specific management options in given locations. Much more important are comparisons of, for example, the value of an increase of a certain quantity of timber with condition A to the value of an increase of a given amount of forage with condition B.

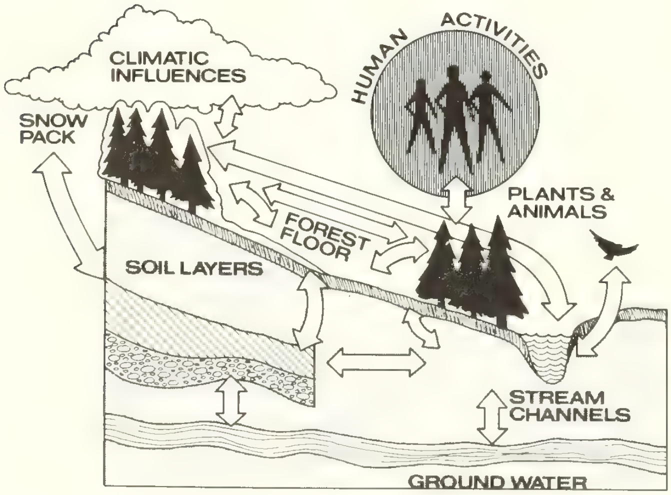


Figure 1.—Complex interactions among natural resources and uses pose important questions that must be considered in the planning process.

A process incorporating this focus involves 1 general steps:

(1) assessing management concerns, publi issues, and resource use and developmer opportunites;
(2) deciding on planning criteria;
(3) collecting relevant data and information;
(4) analyzing the management situation;
(5) formulating feasible, realistic alternative responsive to such assessments;
(6) estimating the physical, biological, social, an economic effects of the alternatives;
(7) comparing the alternatives and evaluatin their differences;
(8) choosing a preferred alternative;
(9) implementing the alternative; and
(10) monitoring the implementation and its effects

These steps are similar to the actions of the plannir process described in the Rules for Land and Resourc Management Planning in the National Forest Syste (USDA Forest Service 1979).

The identification of tradeoffs between the effects possible actions is an important part of step 4, and t evaluation of those tradeoffs is necessary during t formulation of comprehensive alternatives in step Tradeoffs between the effects of the alternatives a identified in step 6, and evaluated in step 7.

Several steps can be carried out concurrently, and may be necessary to return to a step to make change or additions. In fact, the process of steps 5, 6, and 7 ca be cyclical. As step 7 comes into focus, it may becon apparent that alternatives not previously considere are more realistic than those first formulated. Then t process would move back to step 5.

Public land managers are instructed to manage t land to "best meet the needs of the American people and to consider the "relative values of vario resources in particular areas" (from the Multiple U Sustained Yield Act of 1960) in determining the need However, the needs and values are not determined ju by observation of the public's behavior in using t public land and consuming goods and services from t land. More direct public involvement is necessary understand the needs and values, as well as to ta advantage of expertise private citizens have to offe

Public participation is essential to the planning pro ess. Managers must understand public issues a desires for the resources in order to formulate a set feasible management alternatives which provides good basis for comparison, negotiation, and co promise. The interested publics must understand t likely effects of alternative management proposals well as the important tradeoffs in order to provi meaningful input to land managers. Concerned indivi uals and groups must have the opportunity to partic pate in working toward a compromise which accoun for important efficiency and equity concerns.

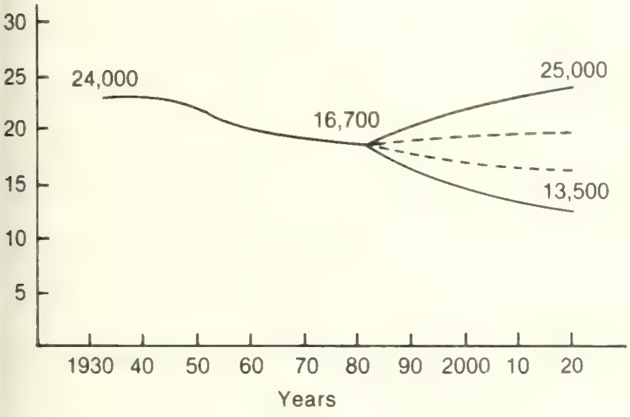
The remainder of this report focuses on steps 4, 5, and 7, using the hypothetical "Ponderosa Forest."

Step 4: Analyzing the Management Situation

The goal of this step is to assess the ability of the lanning area to supply goods and services to society. oods and services are the outputs, or products, which he land, in combination with management, produces. xamples of goods for the Ponderosa Forest are timber, orage, water runoff, wildlife habitat, recreation pportunities, and wilderness preservation. Examples f services are the absorption and breakdown of ollutants and the cycling of nutrients.

Assessing the ability of the area to supply goods and ervices will require determining the potential, or apability, of the land under management to supply oods and services and the appropriateness or suitbility of management practices, considering economic nd environmental concerns and conditions.

The range of feasible output levels for specific goods nd services should be determined. Feasible ranges re determined by the physical, biological, and legal apabilities of the land, and the set of suitable management practices. The capability and suitability onstraints should not include any constraints which re open to question and which therefore are to be ddressed in later stages of the planning process. For xample, since the scenic impact of timber harvesting an issue to be dealt with in evaluating alternatives for managing the Ponderosa Forest, care should be used in placing any esthetic constraints in determining feasible ranges of timber output at this stage in the planning process.



igure 2.—Past and feasible future total annual livestock grazing on the Ponderosa Forest.

One animal unit month (AUM) is equivalent to a cow using the nge for 1 month. Similarly, one cow plus one calf equals 32 AUM's, and a yearling equals 0.8 AUM's.

The figure shows the minimum and maximum amount of liveock grazing feasible in the future, and the rate at which these exemes can be reached. All feasible amounts assume maintenance land productivity.

The minimum assumes gradual drops in expenditures for estock management to the minimum necessary for aintenance of the livestock industry, designation of the roadless eas as wilderness, and maintenance of current overstory denties. The maximum assumes implementation of intensive range anagement practices on the most productive ranges where addinal benefits are expected to exceed additional costs, and duction of overstory densities on harvested areas by 20%. The tted lines show minimum and maximum if all other resource tputs remain at current levels, but expenditures for range anagement vary as with the minimum and maximum.

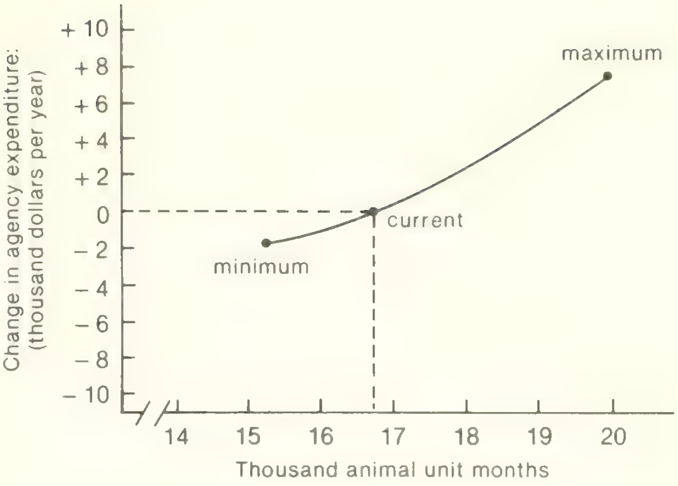


Figure 3.—Change in total agency expenditure resulting from change in livestock animal unit output from current level on the Ponderosa Forest.

It is assumed that output levels of other forest outputs would remain constant while the level of animal unit months changed. Changes in total cost with output increases are the minimum feasible. Changes in total cost with output decreases are the maximum feasible. The changes could not be made in 1 year. See the dotted line portion of figure 2 for details about the feasible rate of change.

The feasible range of output for relevant goods and services can be depicted graphically, as it is for livestock grazing on the Ponderosa Forest (fig. 2). Development of such graphs requires records of past output levels and predictions of how output will respond to management practices. The predictions can be the educated guesses of experts or the result of using more systematic prediction techniques such as computer simulation models. Such graphs should be accompanied by a list of the major relevant assumptions.

The output ranges should be expressed in terms of the cost of implementing them. Ideally, all the costs of production of a specific output would be displayed. This is a difficult task, however, because allocation of some joint (shared) costs (such as the cost of maintaining a road used for both harvesting timber and recreation) is difficult and often arbitrary. It is also unnecessary to display all costs, because the focus in formulating and comparing alternatives is on changes from the present, not on totals. A good option, then, is to display the changes in total agency costs associated with changes in specific output levels (fig. 3). For increases in output levels, the appropriate cost increases are the minimum increases which assure that capability and suitability constraints are met. For decreases in output, the cost decreases are the maximum decreases which assure that the constraints are met.

The assumptions upon which graphs such as figure 3 are based are critical. Figure 3 assumes that outputs of all other resources remain constant. A different cost curve would apply if it were assumed, for example, that overstory (and therefore timber output, wildlife habitat, etc.) also were to change.

In addition to estimating costs of producing at various levels of output, the benefits of various output levels also should be calculated. The benefits should be expressed in monetary terms where possible (fig. 4). Otherwise they should be expressed using other appropriate scales (such as 10-point rating scales). With both cost and benefit information, the manager has a basis for determining what output level, for a given good or service, provides the greatest net public benefit. In some cases, however, non-agency costs, such as the "wear and tear" on private vehicles because of a lesser quality of road construction and maintenance, or the effect on downstream impoundments of increased erosion from forest land, have to be accounted for in addition to agency costs.

The cost and benefit information described above is calculated separately for each resource. Only the minimum necessary assumptions about other resources are made when estimating costs and benefits of a particular output level for a specific good or service. An additional set of information necessary in the analysis of the management situation is that about the tradeoffs between resources.

As with the single resource displays, development of tradeoff relationships requires predictions of how resources will respond to management actions or natural events. Prediction of these relationships generally requires the efforts of an interdisciplinary team, whose task is easier if an appropriate, computerized, multiresource simulation package is available.

Charts depicting tradeoffs can be very helpful in formulating viable alternatives. One type of tradeoff chart (fig. 5) uses individual graphs to show how specific resources might respond to changes in one element of the forest environment—in this case, tree basal area (H. Brown et al. 1974). The chart in figure 5 represents Ponderosa Forest sites with similar soil, vegetation, and weather conditions that are managed under a single set of forest management practices. Similar charts could be developed with an element other than basal area as the common variable.

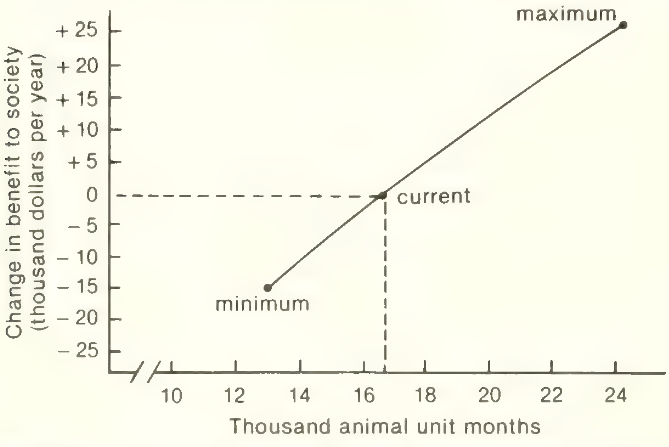


Figure 4.—Change in benefit to society resulting from change in livestock animal unit output from current level on the Ponderosa Forest.

While output levels of other resources may also change in order to bring about some of the indicated changes in animal unit output, these are not accounted for here.

The benefits are based on the value of cattle sold for meat in the market. The changes could not be made in 1 year. See figure 2 for details about the feasible rate of change.

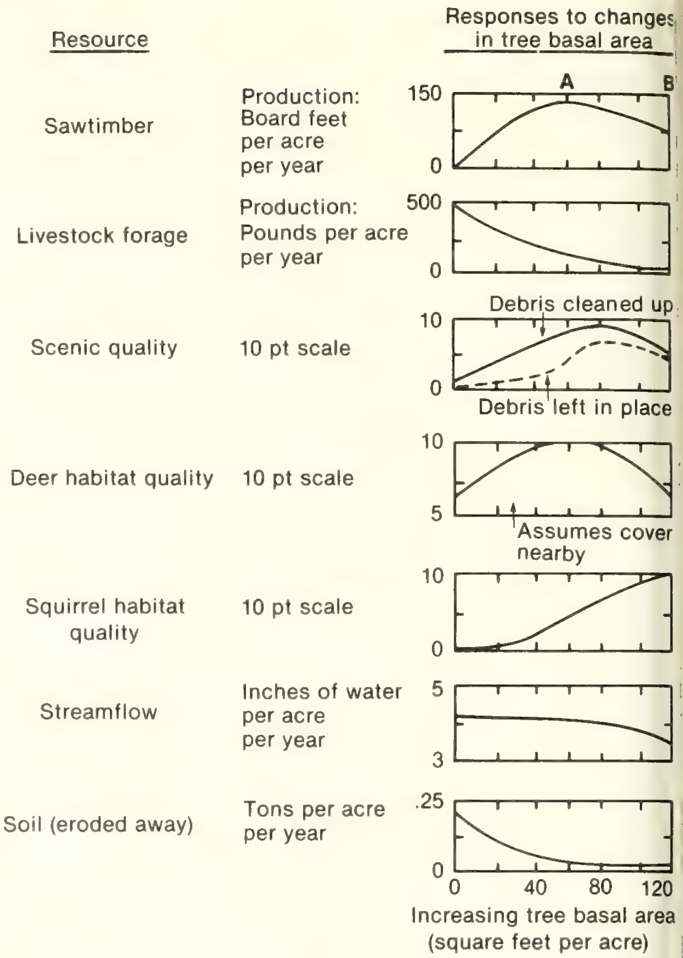


Figure 5.—Individual resource responses on ponderosa pine sites, on Brolliar soils with average annual precipitation from 20-22 inches, managed under the same set of management practices, Ponderosa Forest.

The long-term effects of managing the forest at different basal area levels can be analyzed with this chart. Tree basal area is the number of square feet occupied by living trees on 1 acre of land. Basal area is determined by measuring the cross section of the trunk of sample trees at a point 4.5 feet above ground. In most forests, the trees are not distributed uniformly. Basal area figures usually represent an average for several acres.

For example: An alternative maximizing timber yield—A—would require about 60 square feet of basal area per acre. It would result in fairly low livestock forage production and soil erosion, medium or better scenic quality depending on cleanup of logging debris, high deer habitat quality, and medium squirrel habitat quality and streamflow. An alternative to maximize squirrel habitat—B—would require about 120 square feet of basal area resulting in low streamflow, soil erosion, livestock forage, and deer habitat quality, and medium sawtimber production and scenic quality.

Graphs for other resources and environmental conditions could be developed and added to this chart. Many charts such as this would be necessary to represent the different environmental conditions and management practices found on a large area such as the Ponderosa Forest.

A second type of tradeoff chart combines two, or possibly three, effects in a single graph. Figure 6 shows the tradeoffs between timber production and scenic quality at various basal area levels. Scenic quality in ponderosa pine forests is closely related to tree density, but is also dependent on such characteristics as vegetation growing on the forest floor, amount of fallen trees and limbs, tree size, and density.

A similar graph (fig. 7) displays the tradeoffs between timber production and cattle grazing for a specific set of environmental conditions on the Ponderosa Forest. In addition, monetary value information is utilized to identify that point on the curve which represents the highest economic return.

Step 5: Formulating Alternatives

A set of initial alternatives is formulated considering the management concerns, public issues, resource use and development opportunities, planning criteria, and management situation, including the tradeoffs between effects of possible actions.

The alternatives must be comprehensive, integrated options; they must represent mixes of all the outputs from the planning area. One of the alternatives must represent the most likely conditions expected to exist in the future if current management direction continues unchanged. All other alternatives are considered in relation to this base alternative.

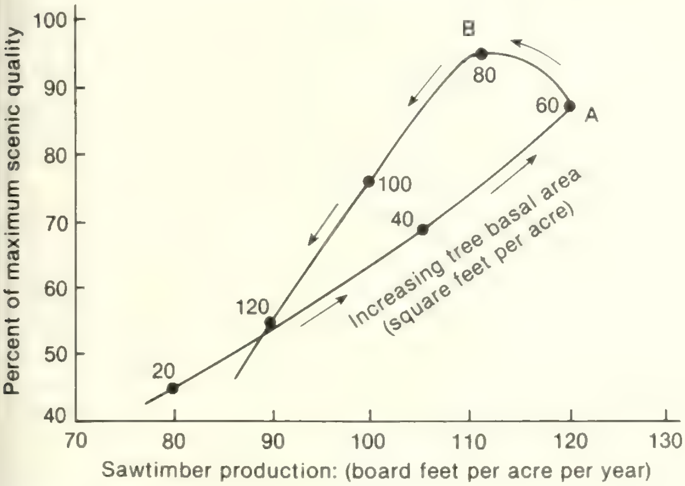


Figure 6.—Dual resource response: Ponderosa pine sites on Brolliar soils with average annual precipitation from 20-22 inches, managed under the same set of management practices, Ponderosa Forest.

Changes in scenic quality and sawtimber production are related to basal area changes on this graph. Moving along the curve in the direction of the arrows represents increasing tree basal area. The amount of vegetation on the forest floor decreases with increasing basal area. Debris from timber harvesting has been cleaned up. All sizes of trees are present.

At point A timber production is maximized; at point B scenic quality is maximized. If timber production and scenic quality are paramount, management options would aim to maintain average basal area between 60 to 80 square feet per acre. All other points on the curve represent less productive combinations of both forest products.

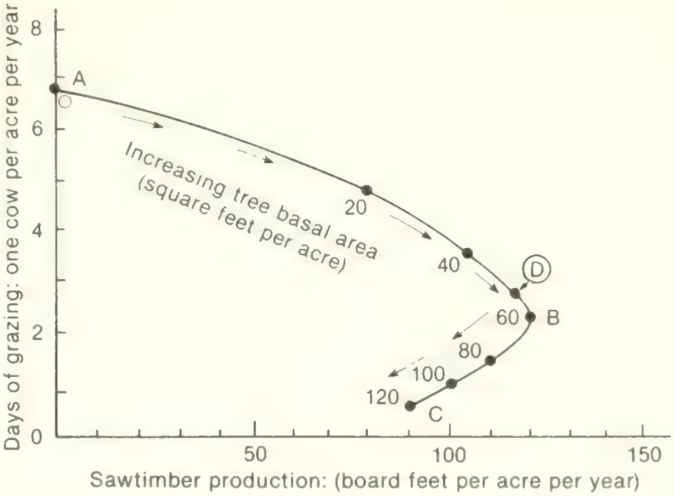


Figure 7.—Dual resource response plus highest economic return: Ponderosa pine sites on Brolliar soils with average annual precipitation from 20-22 inches, managed under the same set of management practices, Ponderosa Forest.

This figure depicts how management of a forest at various basal area levels affects grazing and timber production, and identifies a point of maximum economic return. Moving along the curve in the direction of the arrows represents increasing tree basal area; point A is no trees, point C is dense forest. As basal area increases from A to B, timber production increases while cattle grazing declines; from B to C both decline.

Economic analysis—based on price theory—provides one way to identify the most desirable combination of resource yields where the end products are sold on the open market. Assuming each point on the curve represents equal costs, the total dollar value of grazing and sawtimber in this situation is maximized at point D, where trees cover 57 square feet of basal area per acre. Managed at this level, an average acre of forest should produce 115 board feet of sawtimber, and enough forage for one cow to graze for 3 days, each year.

The set of alternatives chosen at this stage should provide a good basis for comparison and negotiation. They should not encompass the complete range of physically, biologically, and legally feasible possibilities. Instead, they should represent a reasonable range of practical options. Care must be used to not formulate alternatives which either deviate too greatly, or too narrowly, from the "current" alternative.

Comprehensive alternatives which differ both in the agency expenditure level required for implementation, and in the mix of goods and services which would be produced, are difficult to compare if all effects (both benefits and costs) are not expressed on a common scale such as dollars. This is particularly true when local citizens are asked to comment on the alternatives. For example, consider a situation where citizens of "Pineville" are asked to consider a set of alternatives of markedly different expenditure levels, where the alternative with the highest expenditure level would provide high levels of several important outputs. There may be a tendency to prefer the high budget alternative, particularly since the funds to implement the alternative would come from the national treasury.

In such a situation, little might be learned about the more relevant local issue—the relative mix of goods and services.

Where the mix is the relevant issue, all alternatives should require the same expenditure level. If alternative expenditure levels are to be considered along with alternative output mixes and all effects cannot be expressed on the same scale, each alternative output mix should be applied to each alternative expenditure level.

There is no standard approach for formulation. A common approach is to design alternatives to meet different goals, subject to a set of constraints. These goals and constraints reflect information gathered and decisions made during previous planning steps. For example, on the Ponderosa Forest, some goals to be reflected in the alternatives are to increase wood production, increase forage production, increase trail availability, improve habitat for selected species, increase water runoff, and increase acreage designated as wilderness.

Another approach is to include an alternative which maximizes efficiency, subject to a minimum set of binding constraints, along with other alternatives which emphasize equity concerns. This is a feasible approach only where all, or nearly all, of the goods and services affected by the alternatives can be assigned monetary values.

The information generated during the analysis of the management situation is very useful in formulating alternatives. For example, if a goal of one alternative were to obtain maximum sawtimber output subject to a set of constraints, charts such as figure 5 could be used. If the situation were too complicated to be adequately represented in a set of graphic displays, computerized optimization tools, such as linear programming can be used. Optimization tools are particularly useful in allocating resources to meet goals where numerous constraints must be met.

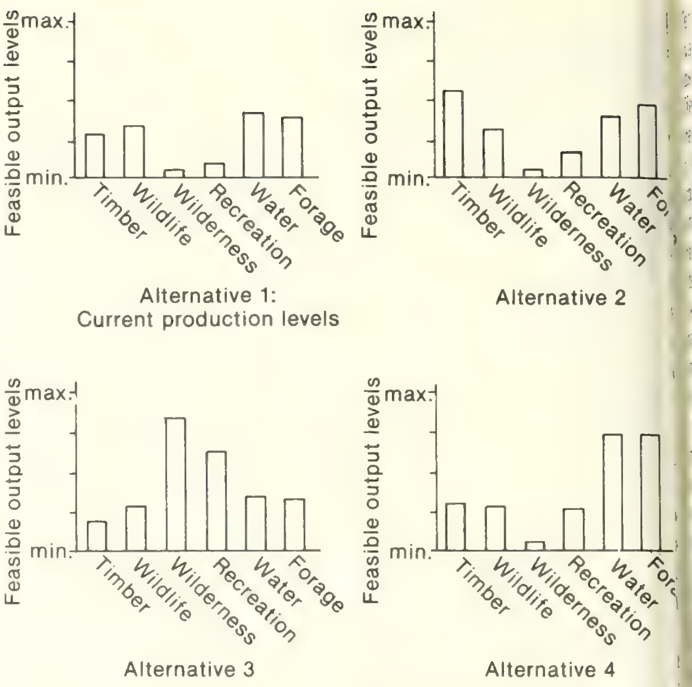
In any case, the set of alternatives should be summarized at the completion of the formulation stage based on a common set of factors such as in figure 8.

Step 6: Estimating the Effects of the Alternatives

Many of the effects of the alternatives are determined during the formulation step, in the process of designing alternatives to meet specified goals. The objective of this step is to more completely and accurately describe effects of the alternatives set forth in the formulation step. The effects of land management alternatives can be broadly categorized as efficiency-related and equity-related.

Efficiency-related effects.—These determine the efficiency of resource allocation, regardless of who gains and who pays. The most efficient allocation is that which maximizes the difference between the benefits and costs, for some set of resources. This difference between the benefits and costs is called the net benefit.

The geographical perspective for efficiency considerations is generally national, rather than regional or local. Thus, efficiency-related effects are estimated to determine how a reallocation of the nation's resources associated with a change in management direction will affect the net benefit of the nation's output; the distribution of that output is not at issue. For a discussion of the efficiency goal see Haveman and Weisbrod (1975).



Alternative 1: Current production levels

Alternative 2

Alternative 3

Alternative 4

Figure 8.—Major aspects of feasible management alternatives for the Ponderosa Forest for 1980-2020.

Each graph shows six bars representing major forest resource outputs. The minimum line represents the level of output for each individual resource regardless of the outcome of the planning process. The maximum line represents the maximum physical, biological, or legal level of output for each individual resource.

Each bar represents a portion of the maximum possible yield obtainable with the respective alternative. Note that it is not possible to attain maximum output levels for all resources at the same time. Increases in one are sometimes accompanied by decreases in another.

These diagrams do not show "how much" is produced. Rather, they illustrate relative changes in production levels and set the stage for more indepth estimations of effects.

Equity-related effects.—These are concerned with who gains from and who pays for resource management actions. Land management decisions may distribute benefits and costs unequally over time to favor present or future citizens; or over space to favor local, regional, or national interests; or they may favor certain social and/or income groups. Equity-related effects are generally displayed in terms of money flows, jobs and opportunities by economic sector, by geographic location, and by times when the effects occur. For a discussion of equity considerations, see Clawson (1975).

Estimating efficiency- and equity-related effects involves three steps: (1) estimating biophysical effects, (2) estimating social and economic effects, and (3) estimating the importance of the effects. Effects on the soil, water, climate, flora, and fauna are biophysical effects. Many biophysical effects affect the way people use the land, and, therefore, cause socioeconomic ffects. The biophysical and socioeconomic effects are f varied importance, or value, to people. For example, onsider two alternatives which affect forest density ifferently over a period of years. The biophysical diferences, such as the number of trees of each size left n a typical acre, habitat conditions for game and ongame wildlife species, and soil erosion rates are important. They are more meaningful, however, when ranslated into socioeconomic terms such as effects on obs, scenic quality, production of wood products, and dispersed recreation opportunities. They are even more meaningful when accompanied by information about how important they are to society—about the value people place on them.

Some of the biophysical and socioeconomic effects of management, such as the effect of harvest on downed wood residues, yields of lumber, and jobs, are rather well understood. Many effects, such as the effect of harvest on some nutrient cycles and habitat for some wildlife species, are not well understood. Decisions must be made on the best information available.

Predictions of the effects are made using a variety of techniques, ranging from sophisticated computer programs with detailed field data to rules of thumb and professional judgment. For all techniques used, the predictions still are best guesses, and should be accompanied by high and low estimates for some degree of confidence. For example, the Ponderosa Forest hydrologist might conclude with 80% certainty that a given treatment will result in an average annual runoff from the area of between 46,000 and 50,000 acre feet, and that a best guess is 48,000 acre feet (table 1).

The importance of the effects is expressed using quantitative scales, such as dollars or 10-point rating scales, where possible. The importance estimates should apply to the biophysical and socioeconomic effects of the alternatives under consideration. While this seems obvious, there are at least three common pitfalls in assigning value estimates. One is to assign a value to an effect, in one location, based on values of the same effect in other locations, where the effect has significantly different values. Another pitfall is to assign value estimates without considering the actual quantities of the outputs which may be affected by the alternatives. For example, although water runoff from the Ponderosa Forest has high value in general, giving much importance to water runoff would be misleading, because the alternatives differ very little in expected runoff quantities (table 1). The third pitfall is to assign value estimates without careful examination of the use of a resource which a change in output level affects.

Table 1.—Selected effects of alternatives: average annual effects of selected outputs from Ponderosa Forest for a 40-year period—best guess and range[1]

	Alternatives			
	1	2	3	4
Sawtimber (million board feet)				
Best guess	21	27	18	29
Range	18-24	24-30	16-20	26-32
Water runoff (1000 acre feet)				
Best guess	48	48.5	48	49
Range	46-50	46-50	46-50	47-51
Forage utilization (1000 animal unit months)				
Best guess	10	23	10	27
Range	8-12	21-25	8-12	25-29

[1] *The range represents specialists' estimates of an 80% confidence interval for the best guess.*

For example, runoff from the Ponderosa Forest has numerous values to downstream users, ranging from a high value for drinking to a low value for irrigating feed grains. However, since the only use affected by a change in runoff quantity is irrigation of feed grains, it would be incorrect to value the runoff change based on its use in the municipal or industrial sectors, or even in irrigating cotton.

As with the biophysical and socioeconomic effects, estimates of importance are best guesses. Upper and lower limits to the estimates, therefore, are generally very useful. The complete set of best guesses and limits allow sensitivity analysis to help isolate the most relevant effects.

Estimating the importance of the total output of an effect is often very difficult. However, estimating the changes from the base alternative resulting from the other alternatives is usually much easier and more reliable. For example, the total value of runoff may be difficult to calculate because of most people's inability to express the importance they place on essential drinking water. However, the value of water for uses generally affected by a small change in the total runoff, such as the value of runoff in irrigating crops or lawns, is much more easily expressed, and more easily quantified using existing market data. Restricting the measures of importance to the differences between alternatives does not diminish the decision maker's ability to compare the alternatives and decide on a preferred course of action, because only the differences are pertinent for the decision. A choice between alternatives is based on the tradeoffs among the alternatives.

Consideration of the efficiency-related effects would be greatly facilitated if a common scale were available on which all costs and benefits could be compared. A common scale would simplify the job of calculating how much of one good or service society is willing to give up to receive a given amount of another good or service.

A monetary scale—dollars—is commonly used for some costs and benefits. Many resource inputs are rather easily assigned dollar values because they are budget items. Some resource outputs, such as timber, water, and forage, are often assigned dollar values because these outputs, or the products made from these outputs, are sold in relatively competitive markets. For example, in Arizona these resources have recently been valued by Kelso et al. (1973), T. Brown et al. (1974), Brown (1976), and O'Connell (1972). Some nonmarket resources also have been assigned dollar values. For recreation examples see Brown et al. (1965), Martin et al. (1974), and Hammack and Brown (1974). The user of such dollar values must be cognizant of the basic assumptions upon which the dollar measures of value are based, such as those regarding the income distribution and the existence of market externalities.

Efforts to assign defensible dollar values to some resources have so far been generally unsuccessful. To evaluate such resources, each must be ranked on a scale of its own. Typical examples are wilderness, wildlife habitat for most species, and scenic quality. Much of the non-monetary value information, chiefly about "environmental values," is obtained using carefully worded questionnaires or observing people's behavior. See Andrews and Waits (1978) for a summary of these topics.

Where two or more products resulting from alternative management proposals can be assigned comparable dollar values, there is a partial basis for decision making, because the relative importance of some of the efficiency-related effects which each alternative produces is known. Nonmonetary-valued resources also can be compared to the monetary-valued resources for each alternative. For example, in providing habitat for a bird that nests in dense pine stands on the Ponderosa Forest, the value of the timber that will not be harvested in order to provide that habitat can be estimated. Then a decision can be made whether the habitat is worth at least as much as the timber which would not be harvested. This is called the opportunities foregone approach. (See, for example, Krutilla and Fisher 1975 or Knetsch and Fleming 1977).

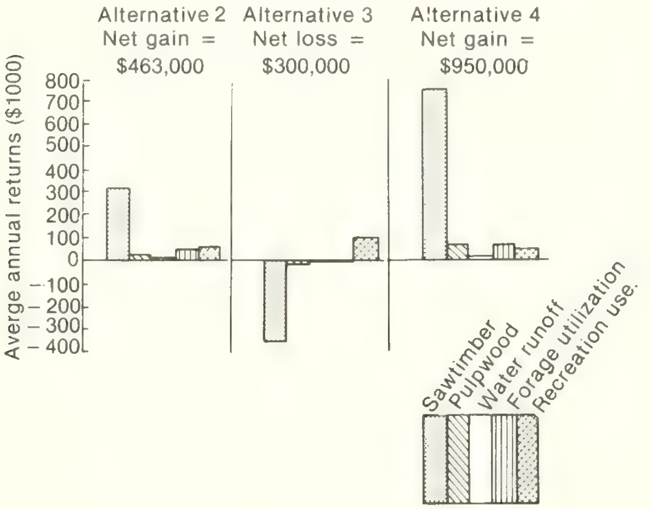


Figure 9.—Anticipated differences in average annual dollar returns over a 40-year period, comparing monetary-valued effects of alternative 1 with alternatives 2, 3, and 4 (5% discount rate), Ponderosa Forest.

This figure illustrates the major differences between the current production level—represented by the "0" line—and the other alternatives. Variations among different products are represented by bars extending from the "0" line.

In this example, when the values of the differences are compared, sawtimber is the most significant of the five dollar-valued products. Pulpwood, water runoff, forage for livestock, and recreation differ little in value. The increase in recreation for alternative 3 is insignificant when compared with the loss of timber value. For another area the situation might be different and recreation might be more important than sawtimber; only by placing the products on a common scale is this obvious.

Note that the water-forage emphasis alternative—No. 4—yields a larger discounted dollar return for sawtimber than the timber volume emphasis alternative—No. 2. A heavy initial harvest is necessary with alternative 4 to increase water and forage. Alternative 2 yields greater timber volumes in the long run.

Standard measures are available, such as the benefit-cost ratio and net benefit measures, to estimate the efficiency of alternatives. Where not all important costs and benefits can be assigned dollar values, however, these measures are of limited use. They can be used to compare alternatives for the set of costs and benefits expressed in dollars, but all the non-dollar-valued effects must be considered separately, or incorporated with the opportunities foregone approach. In such situations, therefore, the primary use of dollar values is similar to that of other importance estimates—simply to help decision makers understand the relative importance of the effects of alternatives. With all available information about the importance of the effects, decision makers hopefully have a sufficient basis for estimating how the alternatives to the base alternative will affect the efficiency of resource allocation.

However, where analysts can at least assign defensible upper and lower limits to the dollar values of all important costs and benefits, estimates of the changes in efficiency of the alternatives compared to the base alternative can be obtained. Such an analysis is accomplished by alternately varying one, or more, of the values while holding the others at their best guess levels. Optimizing tools such as linear programming are very useful for such sensitivity analyses.

Major results of the estimation step, in terms of best guesses, have been aggregated and summarized for a given expenditure level for the Ponderosa Forest in table 2. Alternative 1 is a continuation of current management direction. While most effects are listed as totals for each alternative, some are listed as changes from Alternative 1.

Step 7: Comparing Alternatives

Once the efficiency- and equity-related effects have been estimated, the alternatives must be compared, either to help select an alternative, or to help formulate others. The overwhelming amount of data gathered during step 6 must be condensed to a manageable set of information which describes the key differences between the alternatives. Some information necessarily is lost in the process. Experience indicates that people find it very difficult to compare alternatives on the basis of more than seven or eight effects. Including more may be more detrimental to the decision making process than is the loss of information.

The best guesses and high and low estimates of the effects and their importances provide the basis for sensitivity analyses to isolate the important effects. The

Table 2.—Ponderosa Forest: Average Annual Effects Estimated Over A 40-Year Period

	Alternatives			
	1	2	3	4
EFFICIENCY-RELATED EFFECTS				
Nonmonetary-valued effects				
Wildlife habitat for selected species (10-point scale)				
Deer	9	10	9	9
Elk	9	9	9	10
Squirrel	7	5	7	2
Turkey	10	9	10	9
Timber searching birds	7	6	7	5
Scenery (10-point scale)				
Close-up vantage points	8	6	8	4
Vista vantage points	8	6	8	6
Area of wilderness or potential wilderness (acres)	38,500	38,500	83,000	38,500
Sediment loss (tons)	500	1,130	490	1,660
Monetary-valued effects				
Benefits—physical units				
Sawtimber (million board feet)	21	27	18	29
Pulpwood (1000 cords)	17	25	15	25
Water runoff (1000 acre feet)	48	48.5	48	49
Forage utilization (1000 animal unit months)	10	23	10	27
Recreation use (1000 recreation visitor days)	50	52	60	51
Miles of hiking trail	55	42	135	42
Benefits[1]—value to society ($1000)[2]				
Sawtimber		+ 376	− 535	+ 843
Pulpwood		+ 31	− 17	+ 76
Water runoff		+ 5	− 2	+ 10
Forage utilization		+ 58	− 1	+ 73
Recreation use		+ 57	+ 98	+ 57
Hiking		− 1	+ 98	− 1
Big game hunting		+ 58	NSC[3]	+ 58
Costs[1] ($1000)[2]				
Timber management		+ 67	− 27	+ 112
Roads		NSC[3]	− 150	NSC[3]
Recreation management		− 3	+ 23	− 3
Sediment loss		NSC[3]	NSC[3]	NSC[3]
EQUITY-RELATED EFFECTS				
Monetary-valued effects				
Money flows[1] ($1000 net)[2]				
Federal government		+ 222	− 97	+ 467
Greentree County		+ 3	− 26	+ 52
City of Pineville		+ 0.5	+ 0.1	+ 1.1
Employment (jobs—full time equivalents)				
Pineville area (1980-2000)	589	706	576	798
Metro City area (1980-2000)	421	597	358	637
Community stability[1]				
Human displacement		NSC[3]	NSC[3]	NSC[3]

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[1] *Expressed as a change from alternative 1.*

[2] *Expressed as an annuity at a 5% discount rate.*

[3] *NSC signifies "no significant change."*

most important effects are those which relate to major issues or management concerns, and clearly distinguish between alternatives.

One way to narrow the field is to compare the efficiency-related effects which are dollar-valued. The example in figure 9 emphasizes differences between the current production level and other alternatives for the Ponderosa Forest.

Wildlife effects present a particularly difficult display problem. Alternatives may differ in the effect on 10, 20, or more species. One approach is to use indicator species to represent the effect on several species, such as the use of squirrel habitat as an effect in figure 10. Another approach is to group species, and display average effects for each group (Brown 1974).

The alternatives must be displayed in terms of their important differences. One way to compare the alternatives is to display the total amount of each product estimated for each alternative (fig. 10). The example in figure 10 uses nonmonetary terms.

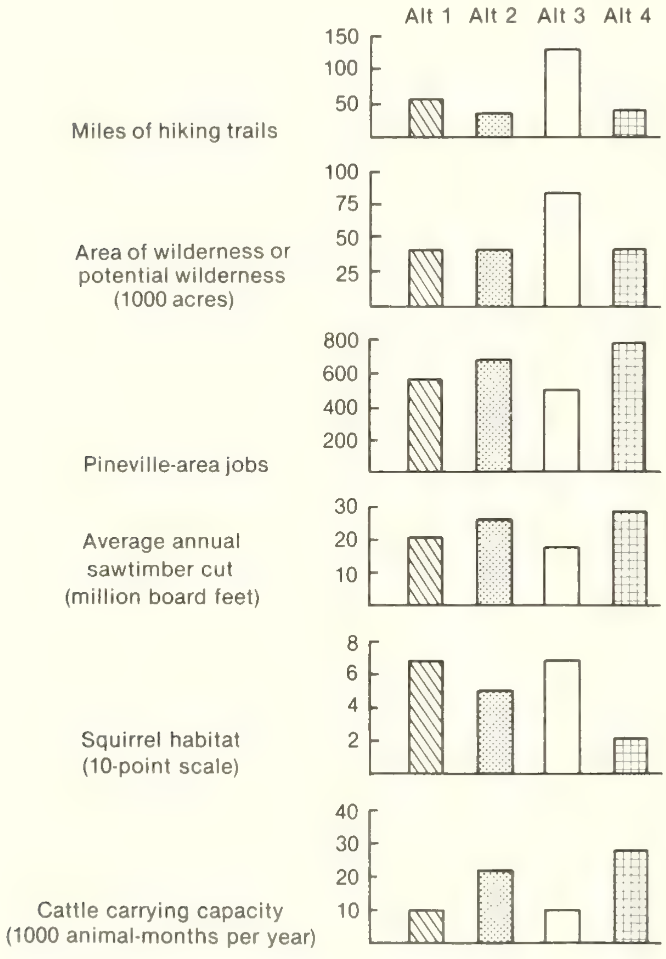

Figure 10.—Anticipated total outputs for products over a 40-year period, Ponderosa Forest.

This figure compares differences among alternatives. For example: gains in hiking and wilderness opportunities realized through implementing alternative 3 can be compared to increased timber harvest and jobs realized through implementing alternative 4.

With these facts, decision makers and interested publics can assess the tradeoffs between alternatives, and decide which values are most important.

Another display for comparing alternatives (fig. 11) uses comparative descriptions and factor profiles (Bishop 1969). The descriptions describe the base alternative and the changes from it resulting from the other alternatives, using a format and terminology designed to focus on differences and to avoid bias. The factor profiles provide a simple picture of the differences, and are suitable for some public involvement activities.

These displays (figs. 9-11) focus on tradeoffs between alternatives. They are only some of many displays which might be used in an actual comprehensive planning situation. While environmental impact statements and other planning documents abound with displays to describe alternatives, little is known about the relative effectiveness of these displays in communicating complex tradeoff information to audiences of varying interest and technical understanding.

Another factor profile tool—called the tradeoff evaluation procedure[2]—is designed for use with small groups of land managers or interested citizens. Currently being tested, this technique allows individuals to specify the amounts of one good or service they are willing to give up for a certain amount of another good or service. The technique provides one way to quantify the relative importance that any individual or group attaches to the products generated by land management alternatives—in effect, putting all such products on a common scale. Where the land management team is using the technique, it would base its importance judgments on the importance information generated during the previous (estimation) step of the process and on its understanding of the issues and political realities involved. A set of such profiles, representing major points of view, could provide the land management team with a better basis for negotiation and compromise in identifying and agreeing on a preferred alternative.

Conclusion

Comprehensive land management planning is a very complex process which depends on judgment at several critical points. Various concepts and procedures can help focus the judgments in a constructive direction. Techniques, some computer-assisted, can be used to predict the effects of alternatives, estimate the importance to society of the effects, and display the alternatives to facilitate comparison. Research is needed to improve the decision making procedures and techniques so that managers have the freedom to focus increased attention on the judgments and public involvement which no procedure or technique can eliminate.

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[2] *Suhr, Lavon L. 1979. T.E.P.: A tradeoff evaluation procedure. (Unpublished manuscript, Intermountain Region, USDA Forest Service. Ogden, Utah.)*

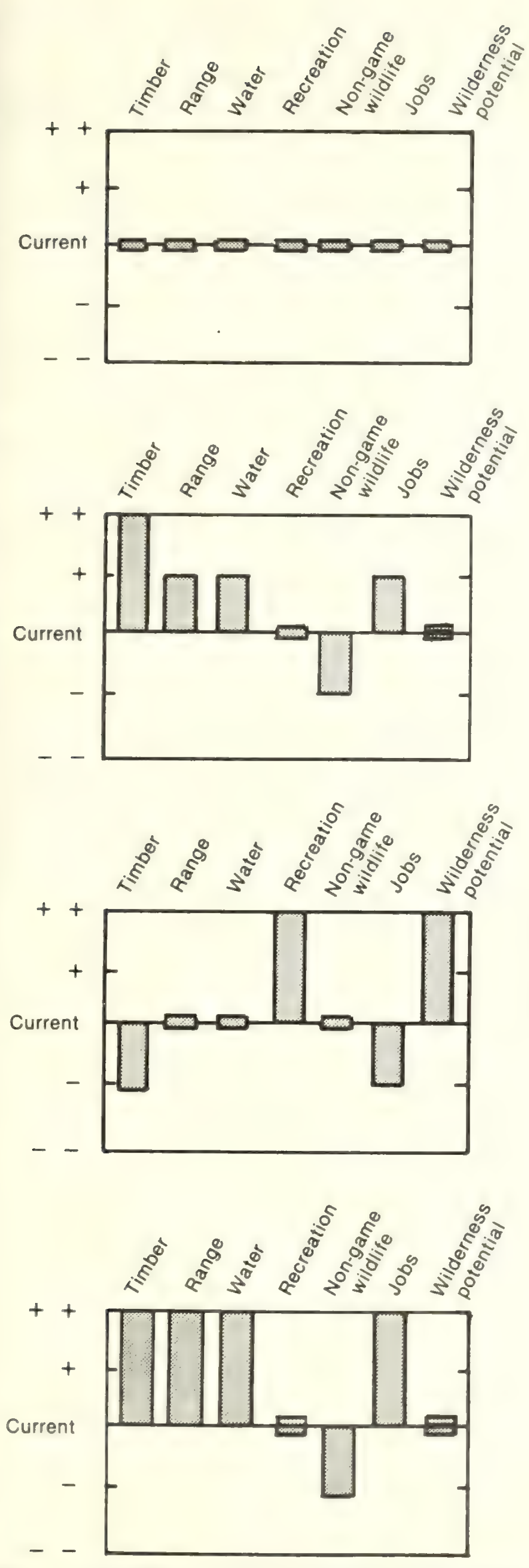

Figure 11.—Comparison of four alternatives on the Ponderosa Forest.

1. Continuation of Current Management. TIMBER—an active timber management program harvests sawtimber and pulpwood by selective cutting on a twenty year cycle. This timber supplies two sawmills and four finishing mills in Pineville. The wood products are distributed nationally. RANGE—Summer cattle range is used by three ranches to support some 2500 animals. Cattle grazing occurs on nearly all of the forest but is concentrated in the southern portion and at lower elevations. WATER—Water runoff from the forest serves the domestic and industrial need of Pineville. Approximately 70% of the water produced on the forest flows to points of use downstream of Pineville including the Metro City dam. The forest is an important source of irrigation water for farms in the area. RECREATION—Recreation opportunities include hunting, backpacking, off-road recreational vehicle use, picnicking, and pleasure driving. There are several maintained hiking trails but no developed campgrounds or picnic areas. The scenic qualities of the physical and vegetative features of the forest attract a large number of recreational users. WILDLIFE—The forest provides wildlife habitat for major deer and elk herds, as well as turkey, squirrel, rabbit, and many non-game birds and mammals. JOBS—Over one-third of Pineville's job force is directly affected by the forest. The wood industry has the greatest economic impact with recreation based trades and services also representing significant economic sources. WILDERNESS POTENTIAL—The forest contains an officially designated wilderness area and an adjacent unroaded area with virgin forests which may have wilderness potential. The current management program will harvest timber from this roadless area during the next forty years by selective cutting.
2. TIMBER production will be increased by selectively harvesting a larger percent of the trees in each area. RANGE capacity will increase as forested lands are opened. WATER runoff will increase slightly. Some types of RECREATION opportunities will decrease due to loss of a hiking trail and the scenic impact of increased timber harvesting. Other types, such as recreation vehicle use, will increase due to road improvement. Non-game WILDLIFE populations will decrease because most species of non-game birds and mammals will lose some habitat. There will be an increase in wood industry based JOBS. The POTENTIAL WILDERNESS area will be harvested by selective cutting, as planned under current management.
3. TIMBER production will decrease slightly. RANGE capacity and WATER runoff will remain unchanged from current management levels. RECREATION opportunities will increase due to additional hiking trails into the unroaded area and to several mountains and lakes. Non-game WILDLIFE populations will be maintained. Wood industry JOBS may decrease, but there may be some increase in recreation-related income. The POTENTIAL WILDERNESS area will not be used for harvests or roads.
4. TIMBER production will increase significantly over the next 20 years due to intensive selective cutting, and then decrease to approximately the present level. RANGE capacity will increase significantly as the forest lands are opened. WATER runoff will increase. Some types of RECREATION opportunities will decrease due to loss of hiking trails in the unroaded area and the scenic impact of increased forest harvesting. WILDLIFE populations for most species of non-game birds and mammals will decrease due to loss of habitat. There will be a significant increase in wood industry based jobs for the next 20 years. The POTENTIAL WILDERNESS area will be harvested by selective cutting, as planned under current management.

The four alternatives are compared here using comparative descriptions and factor profiles. The factor profiles show changes from the current management approach; therefore, all the factors are zero for alternative 1.

In most cases, the "current" or zero point on the factor profile is similar to the current average annual yield for a particular factor. For the wilderness potential factor, the "current" point signifies the progressive harvesting of the unroaded area over the next forty years.

Only non-game wildlife is shown here. Little variation among alternatives is expected for game species.

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Design Criteria for Avalanche Control Structures in the Runout Zone

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Abstract

Guidelines are given for the design and location of deflecting, catching, retarding, and direct protection structures. Terrain, snow conditions, and type and frequency of avalanches are among the most important criteria for planning structural control of avalanches in the lower track and runout zone.

The cover: Earth mounds covered with snow in Glacier Park, Canada. (photo by Peter Schaerer of Vancouver, British Columbia)

Photographs not otherwise identified are by the author.

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NTRODUCTION AND GENERAL INFORMATION

Encounter Probability and Land Use

When land use or proposed land use conflicts with ıe natural avalanche condition, and the encounter robability of an avalanche reaching man and/or his /orks is sufficiently high, avalanche defenses are ssential. The encounter probability E can be com-uted given knowledge of the avalanche-return period in the area of interest and the length of time L that his area will be occupied (LaChapelle 1966). Thus

$$E = 1 - (1 - 1/T)^{L} \qquad [1]$$

he return period is the reciprocal of the probability hat the avalanche will occur during any given year. If, or example, an object is to be located for 30 years at ı spot expected to be reached by avalanches once in 0 years on the average, then the probability of the ob-ect being reached once by the avalanche during this or ny other 30-year period is 0.45 (eq. [1]).

The acceptable value of E is a matter of opinion. In Alta, Utah, for example, computation of E is not made, but private land owners are building new structures where avalanche encounter is a virtual certainty, at Ketchum, Idaho, and Vail, Colo., local authorities consider acceptable only much lower encounter probabilities. Figures 1, 2, and 3 illustrate avalanche-hazard areas. The individual accepting the risk, or the government body controlling land use, must determine what level of risk is acceptable.

If the encounter probability exceeds limits set by individual or government decisions, then the risk is not tolerable, and construction within the avalanche zone should be reduced by prohibiting or limiting construction or by protecting structures through the use of avalanche defenses. Several types of defenses which have been used are discussed briefly in this report.

The design-avalanche concept should be used in planning. A design avalanche is of a magnitude such that it will occur once, on the average, in a period of T years. Thus a design avalanche has an annual probability of $1/T$. The annual occurrence probability does

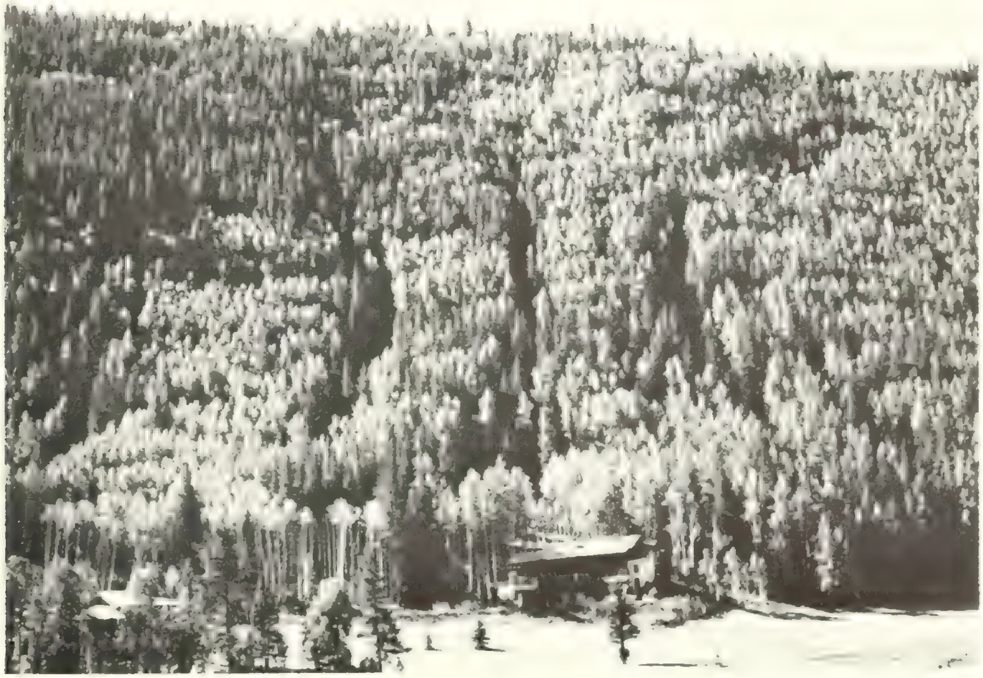

Figure 1.—These small avalanche paths threaten new buildings at Vail, Colo. Although the paths are small and located in the timber, avalanches are known to have reached the sites of the buildings. The duplex on the right is designed to resist flowing-avalanche impact.

not change after an event occurs; therefore, design avalanches are possible on successive years, or even more than once during a single year. Selection of a return period *T* depends upon the type of facilities exposed, but usually varies between 50 and 300 years.

Types of Avalanche Defenses

Several types of avalanche defenses are possible. A decision about what type or types are most appropriate in a given situation should be based on several factors, including the following:

The Type and Intensity of Hazard

The methods used to reduce avalanche hazards depend to some extent on whether mobile or fixed objects are threatened. When mobile objects such as automobiles, railroad trains, and skiers are exposed to severe conditions only occasionally, the hazard can often be reduced by restricting the use of the highways, railroads, or the threatened parts of the ski areas until the avalanches can be released artificially by explosives. This reduces the possibility of damage or injury. Such procedures are common but are not highly reliable in all cases. Effective control requires detailed knowledge of the snowpack, which is not always available to personnel conducting the control operations. Nevertheless, it is possible to remove skiers, automobiles, railroad trains, and other endangered objec while control attempts are made.

Artificial release is usually an unacceptable contr alternative for eliminating the hazard to immovable ob jects such as buildings, bridges, or tunnel portal because avalanches released in this manner may b larger than expected and can destroy the unprotecte structures. Because these objects cannot be remove during times of avalanche occurrence, it must b assumed that natural avalanches which are unmod fied by defense structures will reach the objects, give a long enough time period L. If the encounter probabil ity E is sufficiently high, structural control should b used for protection.

Two broad categories of avalanche-defense struc tures have been used—supporting structures in th starting zone and deflecting or diverting structures i the track or runout zone. The objective of supportin structures is to prevent, or to limit, the size of ava lanche release. Supporting structures anchor the sno to the mountain and alter the stress and deformatio within snowslabs. They are designed primarily fo static loads resulting from creep and glide of th snowpack and the small dynamic loads resulting from small slides between the structures. The Swiss hav gained considerable experience in the design, construction, and maintenance of supporting structure and have developed engineering guidelines for thei construction (Swiss Federal Institute for Snow and Avalanche Research 1961). Design of supporting structures will not be discussed in detail in this publication.

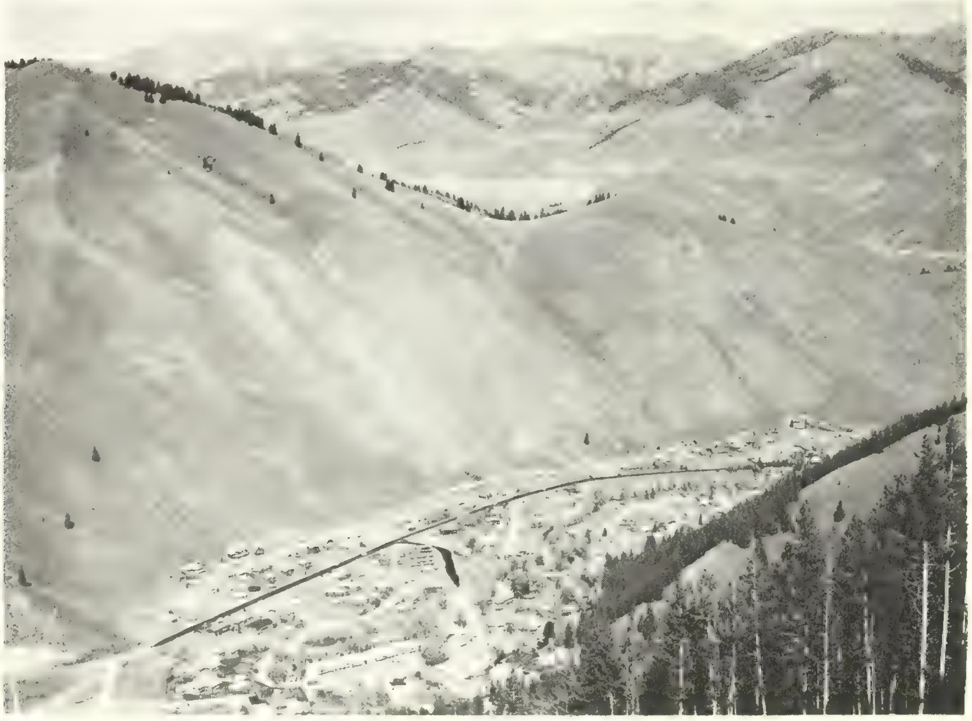

Figure 2.—Severe (but infrequent) avalanche hazard exists in the Warm Springs area of Ketchum, Idaho. Avalanches are known to have traveled 100-200 m out onto the valley floor. Although this is a good location for certain types of avalanche defenses, there has been no systematic attempt to mitigate the avalanche hazard.

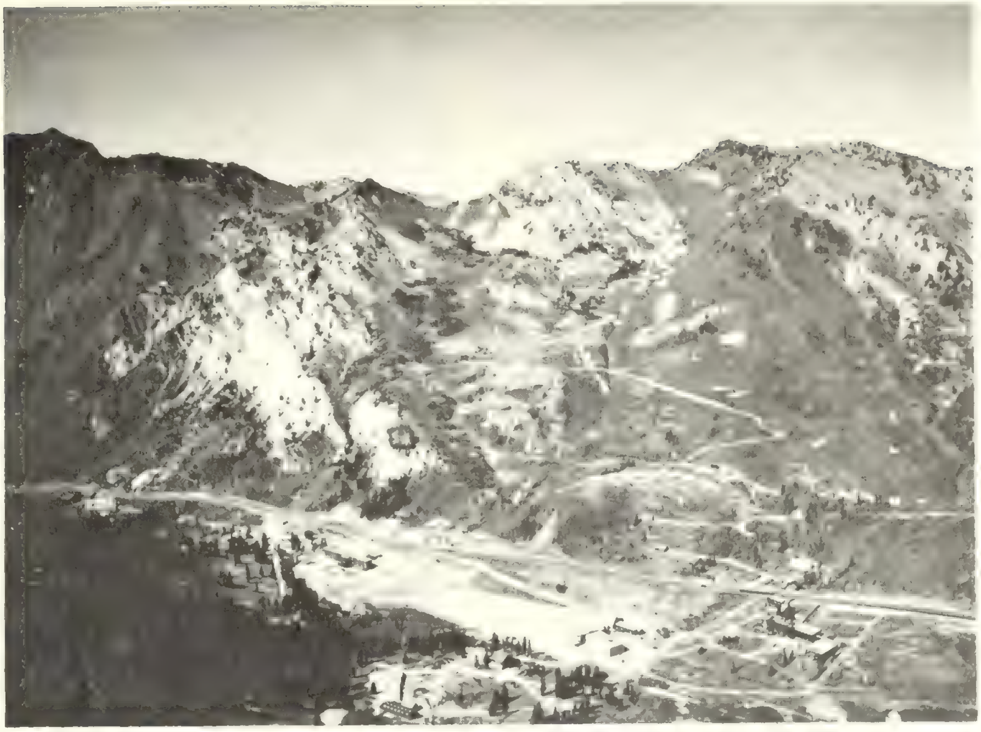

Figure 3.—Large avalanches are known to cross Little Cottonwood Canyon near Alta, Utah, every few years. Buildings and automobiles have been damaged by avalanches in the past. In the future, builders will probably design any new buildings located within designated avalanche paths to resist avalanche impact.

The second type of defense structures are designed to withstand the forces resulting from moving avalanches. These structures are built in the track and/or runout zone (parts of the avalanche path are defined in the next chapter). Several types of track and runout-zone structures are possible, depending on several factors as discussed below.

Avalanche Path Terrain

Avalanche terrain is the first factor affecting the design of structures in the track or runout zone. It is discussed in more detail in the section entitled Design Criteria because it relates to avalanche size and motion; however, designers should ask the following basic questions prior to deciding on the appropriate type of defense:

Are many valuable objects exposed in the runout zone (the location in which avalanches decelerate and stop)? If so, it may not be possible or practical to stop or deflect the flow. Rather, it may be necessary to use supporting structures to prevent or limit the size of the avalanche.

Is the starting zone (the location in which avalanches begin and accelerate) small and well defined? If so, avalanches may be most efficiently prevented by use of supporting structures.

Is the starting zone large but the runout zone long and gradual? If this is the case, it may be possible to dissipate avalanche energy or deflect the flow in the runout zone, thereby protecting some objects.

Is the track confined to a channel or is it unconfined? Confined tracks often discharge onto alluvial fans. Irregularities on the fan surfaces may provide natural barriers to flow, or it may be possible that natural barriers can be enlarged to deflect the flow away from objects.

Economic Feasibility

Early planning and identification of potentially hazardous areas may allow development to avoid avalanche areas completely. In these cases, complete avoidance may be the best and most economical form of defense (fig. 4). However, landowners may not feel this is a viable alternative, based on real estate values. If a decision about whether or not to build avalanche defenses is to be made on purely economic grounds, then it may be useful to compare the cost of defenses to the benefit obtained. Annual cost can be computed by amortizing the initial cost of defense over some time period, such as the life of the structure. Assuming an interest rate, the annual cost can be computed (see Taylor (1964), for example). The benefit would be equal to the annual cost of avalanche damage avoided by construction of the defenses, and is equal to the expected cost of damage times the annual probability of avalanche occurrence. Thus, the benefit/cost ratio, BCR, can be computed

$$\mathrm{BCR} = \frac{\text{annual benefit}}{\text{annual cost}} = \frac{\text{cost of damage avoided}}{\text{amortized construction cost}}$$

Although a benefit/cost analysis may be a rational way to make economic decisions about construction of defense structures, important but less quantifiable factors may be equally important. An unprotected structure in an avalanche zone may be damaged by impact so severely that the occupants are injured or killed. Thus, even if construction of defenses appears economically unfeasible, defenses may be desirable.

Types of Avalanches Expected

The design of structures also depends on the type of avalanche expected. This factor will be discussed in detail in the section on Design Criteria. Certain types of defenses will not be effective against some avalanches. For example, a deep, powder avalanche cannot be stopped or deflected by a low, catching dam or deflecting wall (see sections on Deflecting, Guiding, and Catching Structures). If large, powder avalanches are expected to reach the design point in the avalanche path, then reinforcement of the object may be the only viable type of defense.

Esthetic Considerations

Because avalanche defense structures may have an adverse effect on the environment, esthetic considerations affect the design of control structures. As discussed later, earthen structures need to be quite massive. In some cases, this requires extensive earthwork. Such construction may have an undesirable visual impact and may create new erosion patterns. Early in the planning, designers must give careful consideration to any development in hazardous areas if such development requires avalanche defenses that have an undesirable environmental impact.

In contrast, direct-protection features may be incorporated into the design of structures. Careful architectural design can result in structurally sound buildings with no undesirable visual impact (fig. 29 in the DIRECT-PROTECTION STRUCTURES section). However, for reasons discussed in the section on Direct Protection Structures, direct-protection structures are not always a viable form of avalanche defense.

With all the necessary information about alternative types of defenses at hand, the designer can decide which types of defenses are most suitable at a given site. If track and runout-zone defenses are most suitable, then the designer of the defense must accumulate the necessary design data. This procedure involves calculating the dynamics of the design-magnitude avalanche as discussed in the section on Design Criteria.

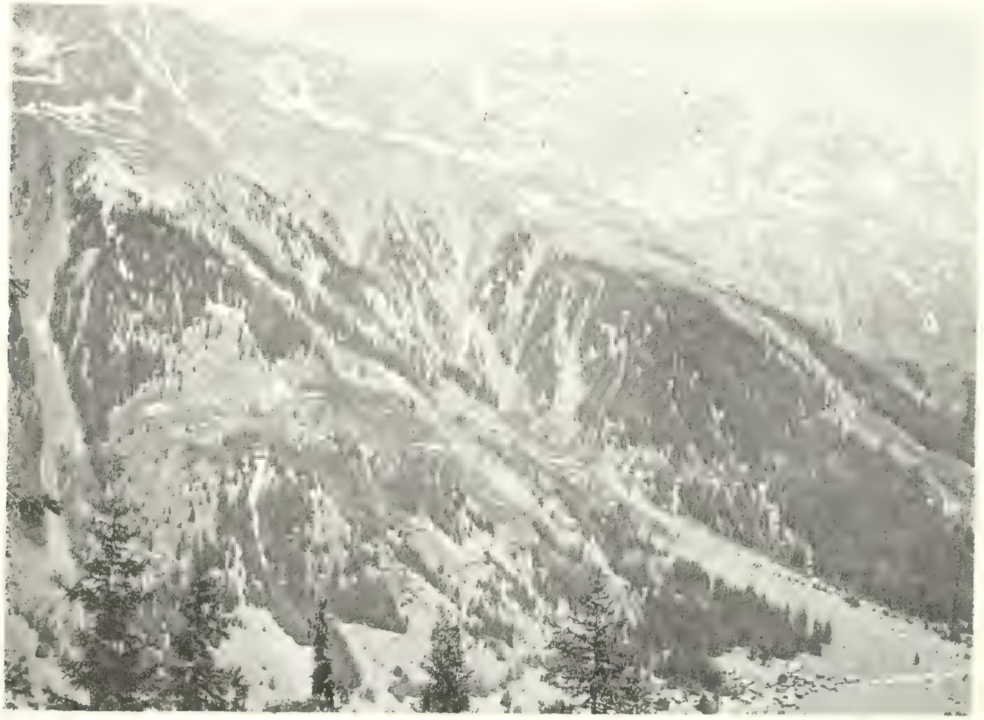

Figure 4.—The village of Monbeil, near Klosters in the Swiss Alps, has been located out of the path of the design avalanche as evidenced by the patch of mature trees above the village. In this case, avalanche mitigation is achieved through avoidance.

nalytical Techniques, Uncertainties, and Limitations

Throughout this paper, suggested design techniques re based upon the characteristics of avalanches and ther factors. The material presented is based on basic uid mechanics applications, measured properties of valanches contained in published or unpublished eports, equations proposed in previous work and ntroduced in this paper, and experience gained in the eld concerning the behavior of avalanches and conrol works. Some of this experience has not been erified quantitatively.

A case in point concerns the computations of design valanche velocities and runout distances, two arameters of prime importance in avalanche zoning nd structural design. Voellmy (1955) first introduced a nodified fluid-dynamic basis for computing avalanche elocity and runout distance. The theoretical validity f this approach has since been questioned by Salm 1966), by Lang and others (1979), and by Perla and thers (1980). However, none of these more recently roposed methods has been calibrated with field obserations of design-magnitude avalanches any more sucessfully than the procedures first proposed by Voellmy (1955). The field calibrations that have been used to test new methods (Lang et al. 1979, Perla et al. 1980) have not reduced the subjectivity inherent in electing important coefficients used in the computaion of velocity and runout distance.

Given all the uncertainties that remain regarding the nethods for computing avalanche dynamics, we present the simple method first proposed by Voellmy 1955), as modified by recent observations (Somnerhalder 1978, Martinelli et al. 1980). The Voellmy echnique still represents the state of the art in avalanche-dynamics technology as well as any other.

DESIGN CRITERIA

Definition of the Design Criteria

The term "design criteria" refers to the physical characteristics of the avalanche that must be considered when specifying defense structure position, orientation, size, strength, and material. The following avalanche characteristics must be known in order to provide the proper design:

Avalanche type (wet or dry snow, loose snow, or slab),
Type of avalanche motion (powder, flowing, or mixed),
Avalanche velocity (the mean velocity at the front of the avalanche),
Avalanche flow height,
Avalanche flow density,
Avalanche discharge (mass per unit time at some location),
Avalanche impact or stagnation pressure,
Avalanche deposit volume, and
Number of avalanches per winter.

These characteristics are obtained through field observations at the area of interest, comparison of this area with other avalanche paths of known characteristics that are located in a similar climate and have similar orientations, terrain configurations, and sun exposures, and through application of equations.

Avalanche researchers recognize that none of these characteristics can be specified with a high degree of precision because we are only learning about avalanche dynamics through present research efforts. Nevertheless, it is essential that we make use of the body of knowledge as it exists today. The fluid-mechanics models of avalanches used most commonly today in Switzerland, Austria, and the United States are crude approximations to a complex, natural phenomenon. In time, more data will be collected, measurements will improve, and perhaps new experiments will be carried out which will affirm, modify, or negate the present model. In the meantime, realizing that the results of the present model are only approximate, land-use planners and designers must make decisions through application of the present state of the art in avalanche dynamics. This is a normal procedure in science and engineering; and, if the procedure is allowed to operate, it will gradually provide improved models upon which more accurate estimates of the magnitude of the design avalanche can be made.

Few data on avalanche velocity, dynamic pressure, density of flow, or length of travel (runout distance) have been obtained with which to advance a single coherent model of avalanche motion or impact. However, research suggests that avalanches tend to behave as fluids or, when velocities exceed roughly 15 m/s, as high-velocity, density currents.[2]

Information Necessary for Structure Design

In order to design structures to withstand, deflect, or stop moving avalanches, we must have information about the following: the total static and dynamic force on the structure, the required size (height, width, and length) of the structure, the volume of avalanche debris in the deposition area, or in the area where the structure will be built, and knowledge of any change in the avalanche direction as a result of the defenses.

This information can only be obtained through analysis of the design avalanche and determination, through calculation, of the avalanche characteristics discussed previously.

Calculation of the Design Avalanche Dynamics

Previous Work

Voellmy (1955) derived the fluid-dynamic basis of snow avalanche motion and impact. His original equations have been modified through subsequent research, but the basic equations and assumptions of Voellmy are widely applied in Austria, Switzerland, Canada, and the United States.

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[2] *Data in files of Arthur I, Mears, P.E., Inc., 222 E. Gothic Ave., Gunnison, Colo. 81230, 1980.*

Sommerhalder (1965, revised in 1971 and 1978) summarized the avalanche dynamics equations commonly applied in the Swiss Alps.

Mears (1976) presented various methods for computing and otherwise determining avalanche hazard through analytical and observational methods.

Leaf and Martinelli (1977) summarized the state of the art in avalanche dynamics equations as developed in the preceding 22 years.

Perla (1980) summarized avalanche release, motion, and impact from a theoretical and practical standpoint.

These publication should be consulted for details on computational techniques and for the theoretical justifications of various assumptions used in computations. A short summary of some of the more important techniques follows.

Dynamics of Flowing Avalanches

Flowing avalanches (from the German *fleisslawine*) refers to the type of motion where most of the mass slides, flows, and bounds within 2 to 5 m of the ground. Although the analytical techniques discussed below assume an avalanche is a continuous, incompressible fluid, it should be remembered that real avalanches consist of fragments of the slab. These fragments may range in size from finely pulverized snow to chunks more than 1 m in length. A hard-slab release may produce an avalanche that is a cascade of large slab fragments and does not resemble a fluid, while a soft-slab avalanche may become quickly pulverized int small fragments suspended by air turbulence. In th first case, a fluid model may be inappropriate (fig. 5 while in the second case, it may be acceptable (fig. and 7).

According to the fluid-dynamic theory, which ha been adapted from empirical studies of water flow i open channels, the maximum velocity of a flowin avalanche is computed as

$$V = [\xi h' \ (\sin \alpha - \mu \cos \alpha)]^{1/2} \qquad [2$$

where h' is the flow height, ξ is a turbulent frictio coefficient, μ is a sliding friction coefficent at the bas of the avalanche, and α is the slope angle. In practic equation [2] is usually applied several times over a lon avalanche path of complex topography and varyin longitudinal gradients. In each case $\xi h'$, μ, and α wil have different values depending upon slope, roughness, and entrainment of new snow into the avalanche

Table 1 provides estimates of the parameters o equation [2] based on a synthesis of field work conducted in the United States and Canada (Schaere 1973, Martinelli et al. 1980). The flow height h' is given as a multiple of the mean fracture height h_0; both h' and h_0 are measured perpendicular to the avalanche running surface.

In the original Swiss work (Voellmy 1955, Sommerhalder 1965), it was assumed, for unconfined avalanches, that the flow height of the avalanche, h', was approximately equal to h_0, the height of the released slab. However, recent research in the United States suggests that dry, soft-slab avalanches disintegrate

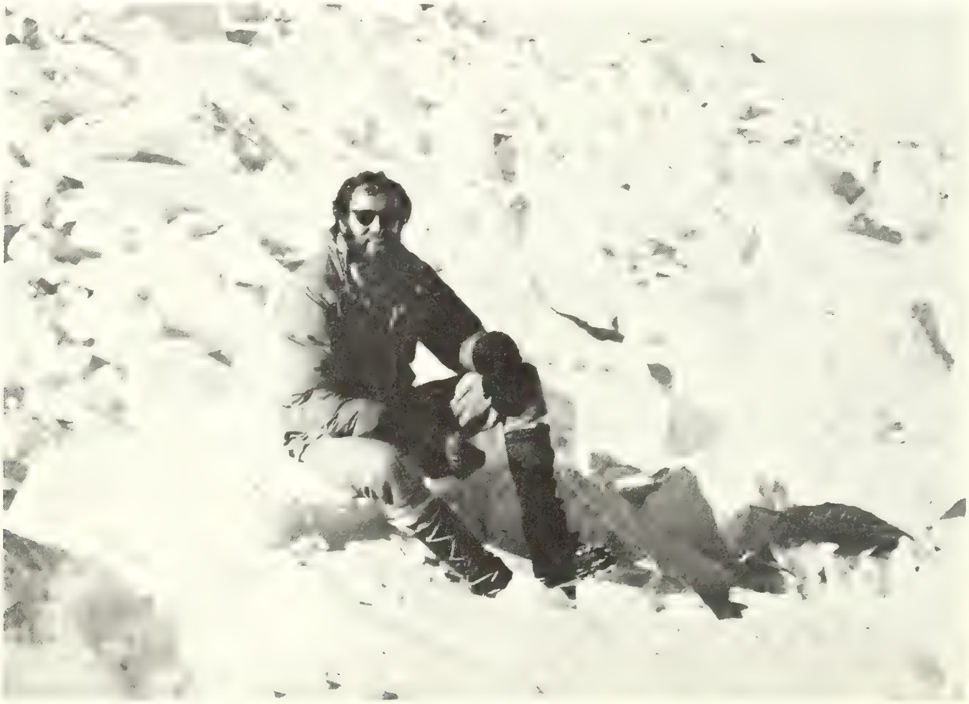


Figure 5.—This hard slab avalanche consisted of large fragments. In such cases a fluid-dynamic model of avalanche motion is not appropriate.

and disperse upward after a short running distance. Thus, it is not justifiable to assume $h' = h_0$. Typical values of the ratio h'/h_0 are related to avalanche type in table 1. In general, dry, soft-slab avalanches attain greater flow depths than dry, hard-slab avalanches, and larger, higher velocity avalanches attain greater flow depths than smaller, slower avalanches of the same type.

Prior to application of equation [2], the designer must determine the type of snowslab expected to be released from the starting zone during design avalanche conditions. This can be done from avalanche and meteorological records and through discussions with observers. (Examples of starting zones are shown in figures 8, 9, 10.) Variation in ξ and μ also strongly affect the computation of velocity. The smaller values of ξ apply when the avalanche falls through rough terrain with many trees and rock outcrops, and the larger values apply when avalanches run on smooth surfaces such as old avalanche debris. The range in μ varies by a factor of three in response to snow type, terrain, and possibly degree of slab fragment dispersion in the flow (Mears 1980). In general, μ is probably small in large avalanches and the product ξh is large.

The bulk density of a flowing avalanche should be proportional to h_0/h'. Thus, with $100 \leqslant \rho_0 < 300$ kg/m³, and $1.0 \leqslant h'/h_0 \leqslant 5.0$, the bulk density, ρ, of the flowing snow can range 20-300 kg/m³; ρ_0 is snow pack density. Bulk density probably decreases with distance from the ground in dry-snow avalanches, and the mean forward velocity probably increases with distance above the ground. For design purposes, it is probably acceptable to assume a uniform density of 100-200 kg/m³ for dry-flowing avalanches throughout the depth of flow. The larger value should be assumed for smaller, lower velocity avalanches, and smaller values for higher velocity avalanches.

Avalanches decelerate and stop in the runout zone as the kinetic energy of flow is gradually dissipated through friction over some distance S known as the runout distance. Equating kinetic energy to work done through flowing and sliding in the runout zone yields Voellmy's (1955) expression for runout distance

$$S = \frac{V_0^2}{2g(\mu \cos\beta - \sin\beta + V_0^2/2\xi h')} \qquad [3]$$

where V_0 is the velocity at the beginning of the runout zone and β is the mean slope of the runout zone. For large, dry-snow avalanches, it should be assumed that the runout zone begins when the slope angle decreases to 15-20°. Such avalanches may run for 1,000 m or more on slopes of 10° or less. However, selection of a reference position for the beginning of avalanche deceleration is sometimes difficult and subjective, particularly in avalanche paths with gradually decreasing longitudinal gradients. The beginning position of deposition is thought to correspond to the beginning of final deceleration (Mears 1980).

If wet-snow avalanches are known to be the design case, then flow work will not be an important energy-dissipative mechanism in the runout zone and may be

Table 1.—Suggested values of coefficients used in equation [2]

Avalanche type	ξ	h'	μ
	m/s^2		
Thick, hard slab	400-600	$h_0 - 2\,h_0$	0.15–0.30
Soft slab	400-1,000	$1.5\,h_0 - 5\,h_0$	0.10–0.30
Wet slab	400-600	$h_0 - 2\,h_0$	0.10–0.20

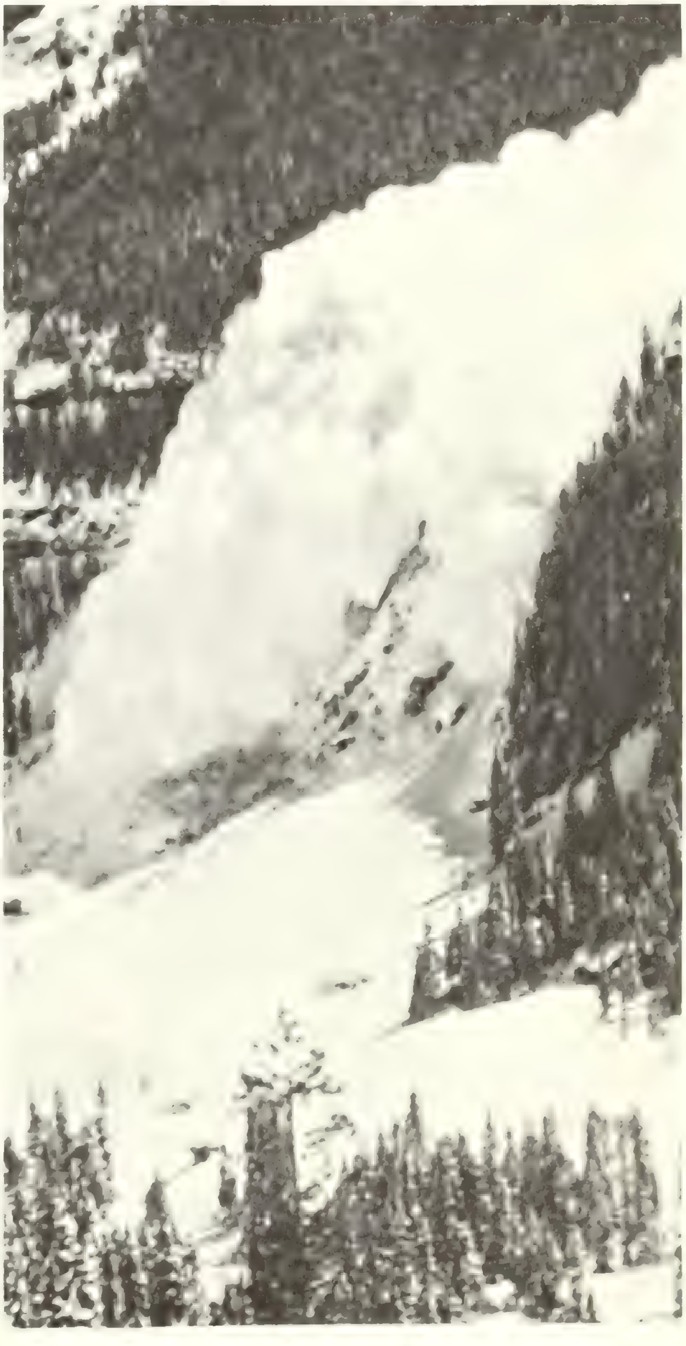


Figure 6.—Most of the flowing mass of dense snow in this mixed motion avalanche is obscured beneath a deep, diffuse cloud of small snow and ice particles. (Schoolhouse Avalanche near Camp Bird, Colo. Photo by Johnny Johnson Petley Studios, Ouray, Colo.)

disregarded in equation [3] provided $V_0 < 10$ m/s. Thus, the runout distance for wet-snow avalanches, S_w, is computed simply as

$$S_w = \frac{V_0^2}{2g(\mu \cos\beta - \sin\beta)} \qquad [4]$$

Equations [3] and [4] should be applied only when $\mu > \tan\beta$. In contrast, when $\mu < \tan\beta$ and $S_w < 0$, the avalanche is still in steady flow and will not stop in that section of the path.

Often avalanche defense facilities will be planned within the runout zone. For the proper design of such structures, the designer must determine the avalanche velocity at some point within the runout zone. If total frictional work against the flow is assumed constant across the runout zone, then it may be assumed that the dissipation of kinetic energy is constant with distance traversed. From these assumptions we can determine the velocity, V_x, at some point a distance, x, into th runout zone as

$$V_x^2 = V_0^2\,(1\text{-}x/s) \qquad [5$$

Analysis of Channelized Avalanches

Channelized avalanches require a different method of analysis because the snow released in the starting zone is laterally confined in the track and one can no longer analyze motion on a per-unit width basis. Field observations suggest that the flow height h' within channels below large starting zones is substantially larger than those suggested in table 2 for nonchannelized avalanches. In such observations, however, it is difficult to distinguish powder-blast damage (discussed below) from flowing avalanche damage; thus, results obtained through application of equations [6]-[10] should be considered approximations. Usually, flow

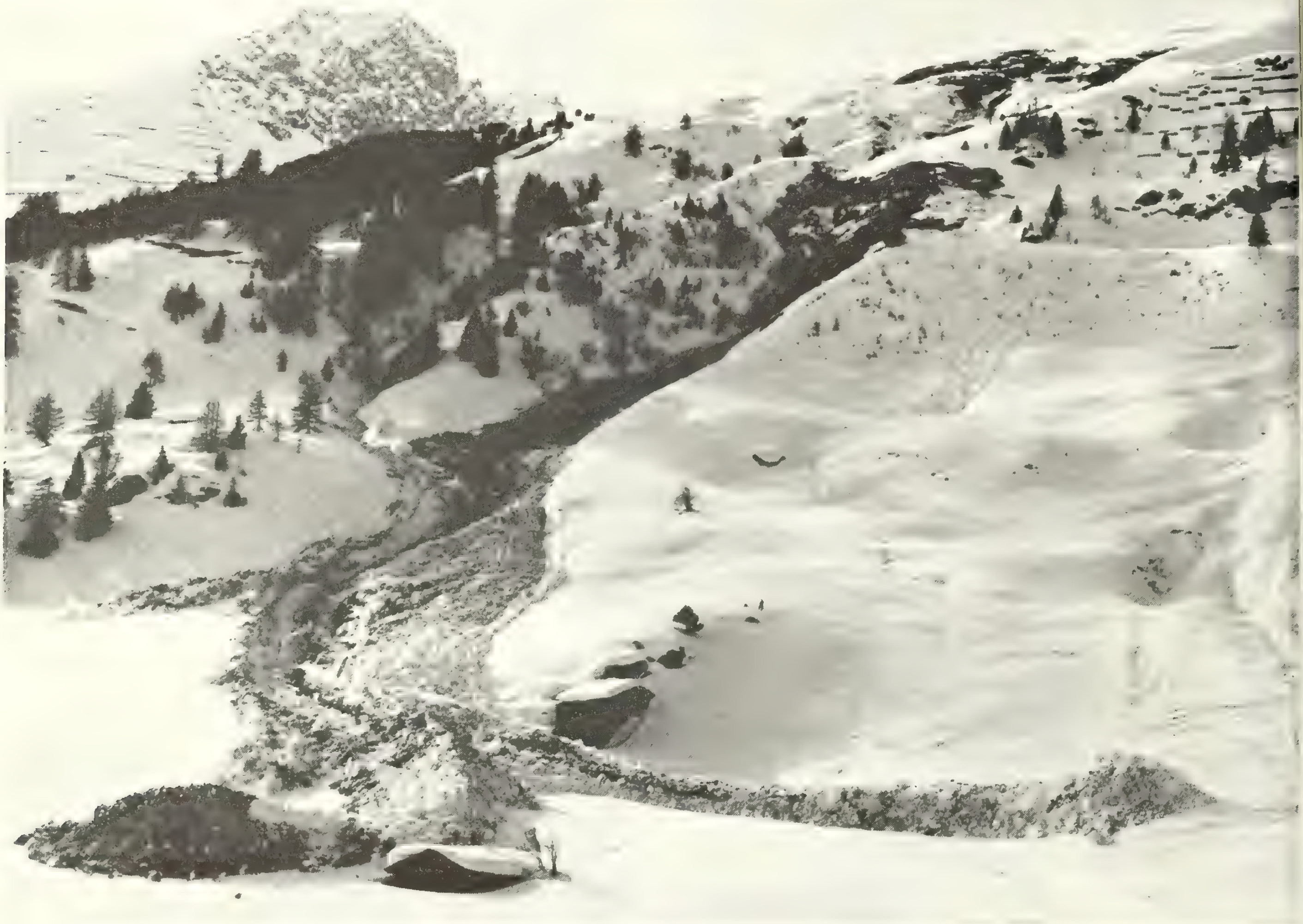


Figure 7.—A wet-snow avalanche moves slowly and has a smaller flow depth than large, dry-snow avalanches. The direction of wet-snow avalanches can be changed because of their moderate velocities (photo taken near Davos, Switzerland, by Andre Roch of Geneva).

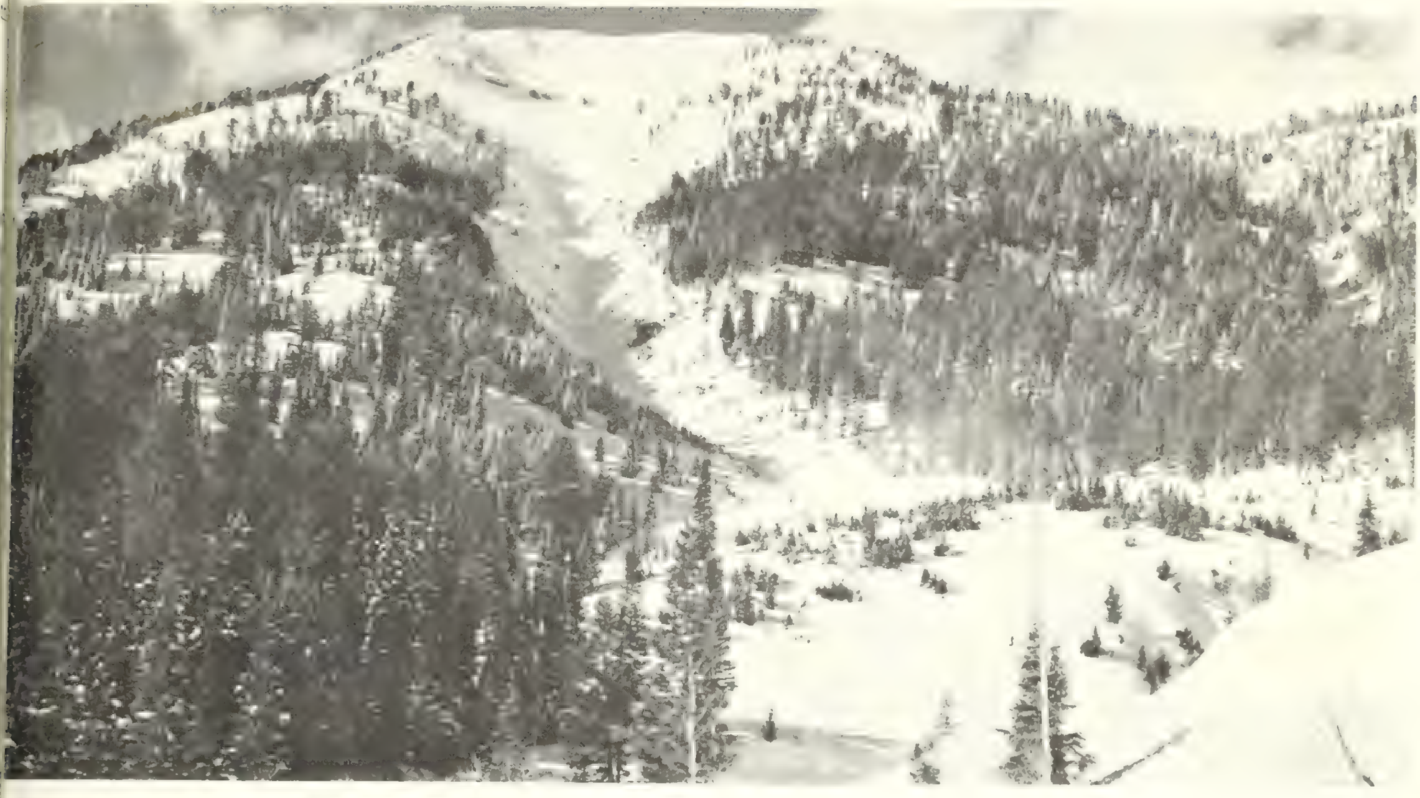


Figure 8.—The smooth, and broad starting zone of this avalanche path is above timberline. During design-avalanche conditions, a large slab may be released from the entire starting zone. (Glory Hole Avalanche, near Wilson, Wyo.). Photo by Hans Frutiger.

depths and velocities are larger and runout distances are greater when a given volume of snow flows down a channelized track than when it flows down an unconfined slope.

Figure 11 illustrates a channelized avalanche path below a large starting zone. A large release of snow of volume K in the starting zone will produce a large discharge rate Q in the track where the flow is confined. It is assumed that the mean discharge from the starting zone equals the mean discharge through the confined section of the avalanche track. If the discharge in the track is large, this forces the flow height and hydraulic radius to be large also. For the channelized avalanche case, the flow depth h' in equation [4] should be replaced with the hydraulic radius R so that the terminal velocity becomes

$$V^2 = \xi R(\sin \alpha - \mu \cos \alpha) \qquad [6]$$

Equation [6] indicates that the terminal flow velocity is proportional to the square root of R. The term $(\cos \alpha)^{1/2}$ varies by only a small amount across the range of slopes on which large avalanches occur (Bovis and Mears 1976), and the term $(\mu \cos \alpha)^{1/2}$ may become insignificant at high velocities.

The physical dependence of R on starting-zone area is best illustrated by combining equation [6] with the continuity principle of hydraulics. For a given starting-zone area A and height of released snow slab h_0 the volume K of snow released is

$$K = Ah_0 \qquad [7]$$

As discussed by Salm (1975), the volume K is completely discharged through the starting zone when the upslope margin of the detached slab has traversed the slope distance L measured from the top to the bottom of the starting zone. The time required to discharge the slab from the starting zone is

$$t = L/V \qquad [8]$$

and the mean discharge rate during this time, t, is

$$Q = K/t \qquad [9]$$

Continuity requires that this Q also be conveyed through the channelized track if it is assumed that deposition and entrainment within the track are equal. Within the track

$$Q = A_t V_t \qquad [10]$$

where A_t is the track cross-sectional area at a given point, and V_t is the average flow velocity through this cross section. Because A_t and R are related through cross-section shape, and V_t is a function of R from equation [6], equations [6] and [10] must be satisfied simultaneously, specifying both cross-section area and avalanche velocity through a given cross section.

An accurate estimate of the starting-zone area A and the release volume K is critical in an analysis of this type. Observations of large avalanches (Mears 1980) suggest that there be net removal of snow on slopes of 30° or steeper, and that deposition and entrainment of new snow become approximately equal on slopes of 20-30°. Thus, for purposes of design, it should be assumed that the starting zone (the area of the avalanche path contributing to K) consists of all slopes steeper than 30° that can release during design-avalanche conditions.

Powder Avalanche Dynamics

Powder avalanches are deep, high-velocity, low-density suspensions of small snow and ice particles in air. They result from disintegration of dry snow slabs and often accompany high-velocity, dry, flowing avalanches. Powder avalanches can form readily when dry, flowing avalanches fall over cliffs and additiona air is entrained into the flow (fig. 12).

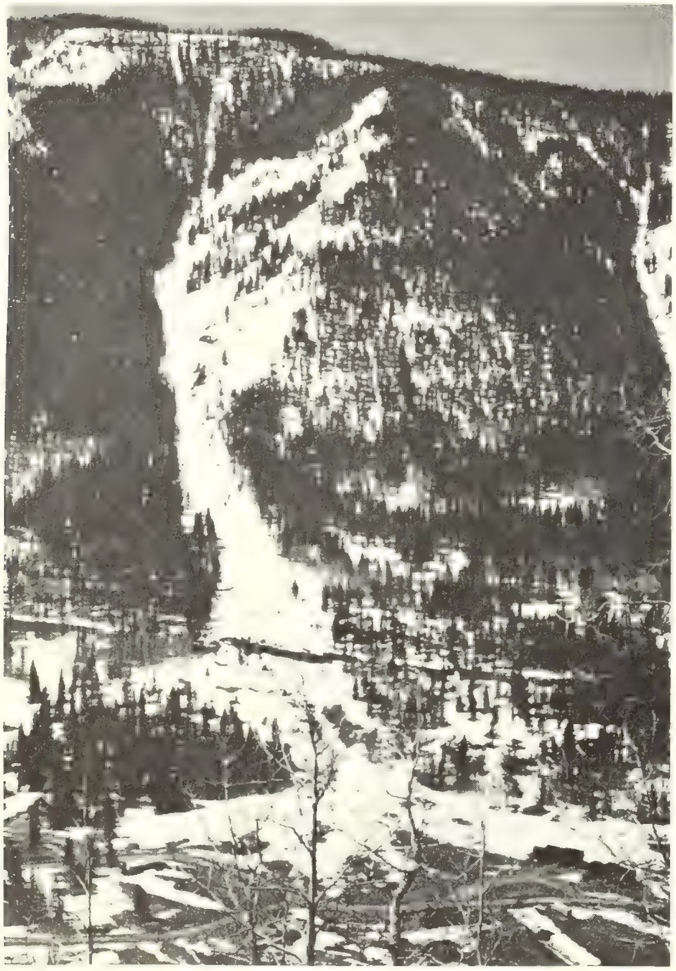


Figure 9.—The starting zone of this avalanche path is below timberline. Even during design-avalanche conditions, much of the snow within the starting zone will remain anchored to trees and terrain irregularities. (King Arthur's Avalanche, Vail, Colo.)

Powder avalanches are likely whenever the maximum velocity of dry, flowing avalanches exceeds roughly 30 m/s. At high velocity, energy dissipation within the flow causes larger chunks of the slab to become progressively fractured into smaller and smaller particles until a density current of snow mixed with air accompanies the denser mass of flowing snow In this way, a powder avalanche becomes separated from the flowing avalanche, attains higher velocity and reaches the runout zone several seconds prior to the main mass of the avalanche. At such high velocities and flow depths, powder avalanches will flow much longer distances into the runout zone than flowing avalanches.

It should be assumed that powder avalanches can form and be a part of the design-avalanche condition wherever moderate to large flowing avalanches can be expected. Following the definition of Frutiger (1964), medium-sized avalanches have starting zones of from 3×10^4 to 12×10^4 m^2 (7-30 acres). Large starting zones may, during favorable conditions, produce dry avalanches that move as flowing, mixed motion, or powder avalanches. This must be considered in the design of defense facilities.

Typical values of velocity, bulk density, and flow height for moderate to large, powder avalanches are given in table 2. The density values are only estimates, since no measurements have been made.

In an unrestricted runout zone (where runout distance is not limited by the opposite valley wall, for instance), it should be assumed that powder avalanches will travel considerably farther into the runout zone than flowing avalanches. It is not possible to compute the runout distance of powder avalanches. Some approximate guidelines can be given, however, to compare the runout distance of powder avalanches S_p with the runout distance S of flowing avalanches. As discussed earlier, S is computed through use of the methods discussed previously. These comparisons are valid only for the same avalanche path; thus, it is necessary to first compute or otherwise determine the flowing avalanche runout distance S and add to that the runout potential of the powder avalanche. Suggested differences between S_p and S are given below:

Avalanche size classification	S_p-S
Moderate	50–150 m
Large	150–300 m

Many avalanche runout zones are affected by both flowing and powder avalanches, which may be either wet or dry. Different types of avalanches can be expected to reach different parts of the runout zone (fig. 13).

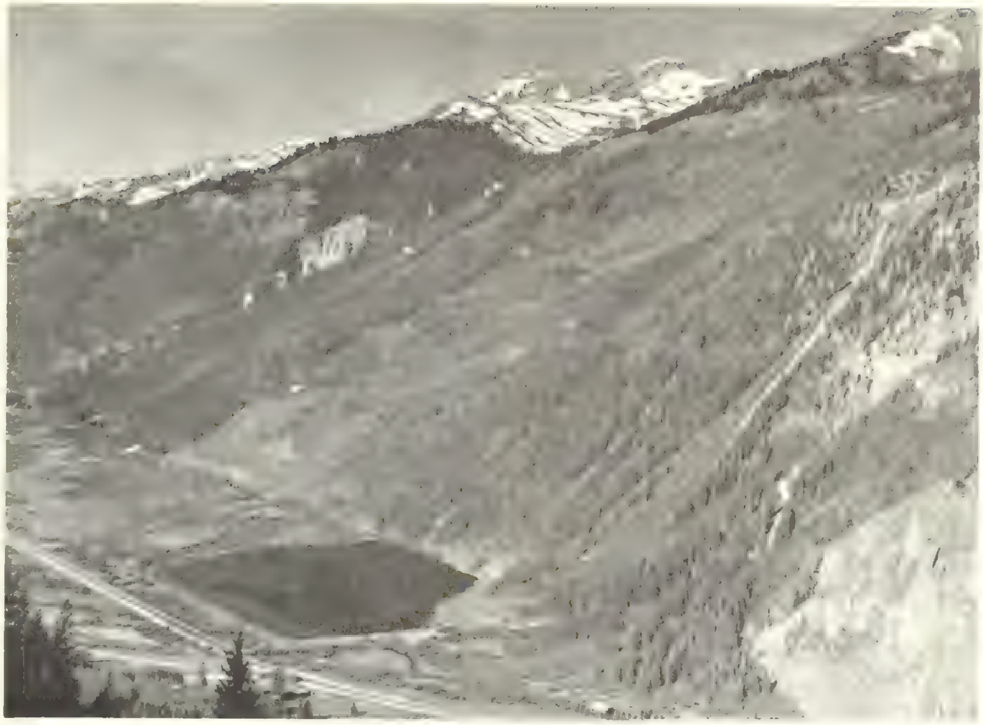


Figure 10.—Avalanches on this unconfined avalanche path are known to have crossed the highway a distance of 350 m from the break in slope. In unconfined avalanche paths, the velocities and runout distances are not dependent on the width or area of the fracture. (Ironton Park, San Juan Mountains, Colo.)

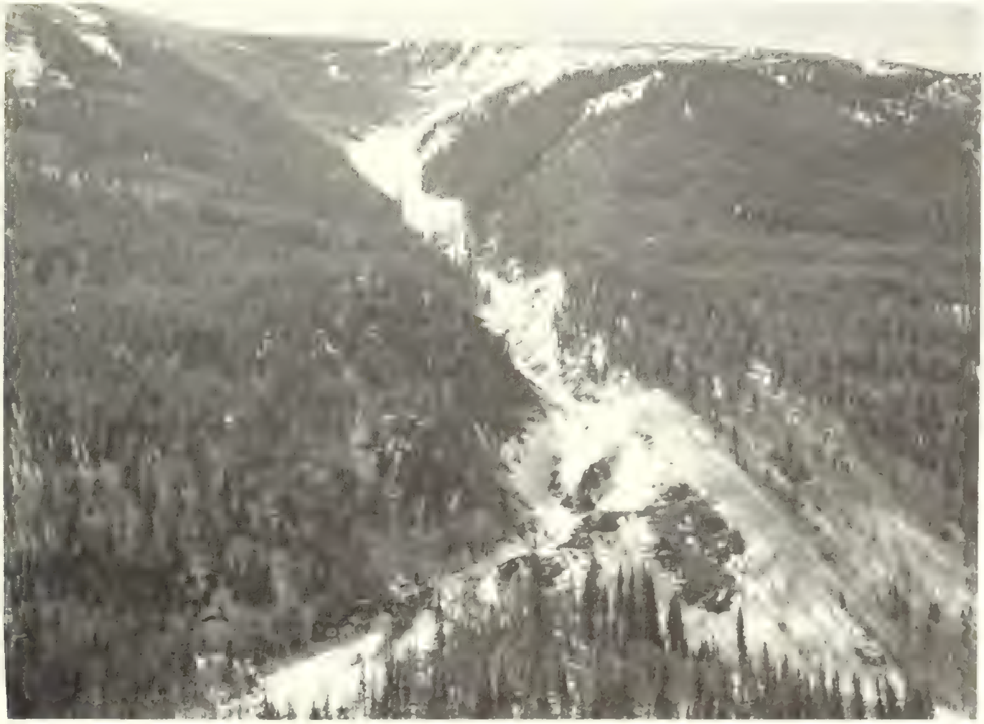


Figure 11.—The velocity and runout distances potential of avalanches in this confined path depend partly on the volume of snow released from the starting zone. (Deadman Gulch near Silver Plume, Colo.)

AVALANCHE IMPACT

Knowledge of probable avalanche impact pressures is important in structural design. As discussed previously, fluid-dynamic models are commonly used in calculations of avalanche velocities and runout distances. Using this convenient simplification, avalanche impact can be modeled as the impact of a fluid with a stationary, rigid object. Such an assumption is justifiable for most avalanches, but it is important to recognize the limitations of this approach because of the variability of avalanche types, densities, velocities, and particle sizes.

Fluid Model

For an avalanche to be adequately modeled as a fluid, it is necessary for the snow and ice particles comprising the flow to be small, compared to the size of the impact area considered. Preliminary analysis indicates that a fluid-impact model is appropriate for powder avalanches and dry-snow avalanches in which most of the avalanche mass consists of particles less than about 10^{-4} m^3 in volume as long as the velocities exceed about 15 m/s. Most dry, soft-slab avalanches and powder avalanches satisfy these conditions; wet-snow avalanches and hard-slab avalanches probably do not. At velocities of less than 15 m/s, dry-snow avalanches may cease to flow as a fluid and begin sliding as rigid bodies. Thus, at low velocities, a fluid-impact model may not be accurate, as discussed below.

If an avalanche is modeled as a fluid of density ρ' moving at a velocity V, then the impact pressure P is determined by an expression of the form[3]

$$P = K\rho' V^2 \qquad [11]$$

where K is a dimensionless coefficient that depends on the details of the impact, the internal structure of the avalanche, and the shape of the object.

Powder Avalanche Impact

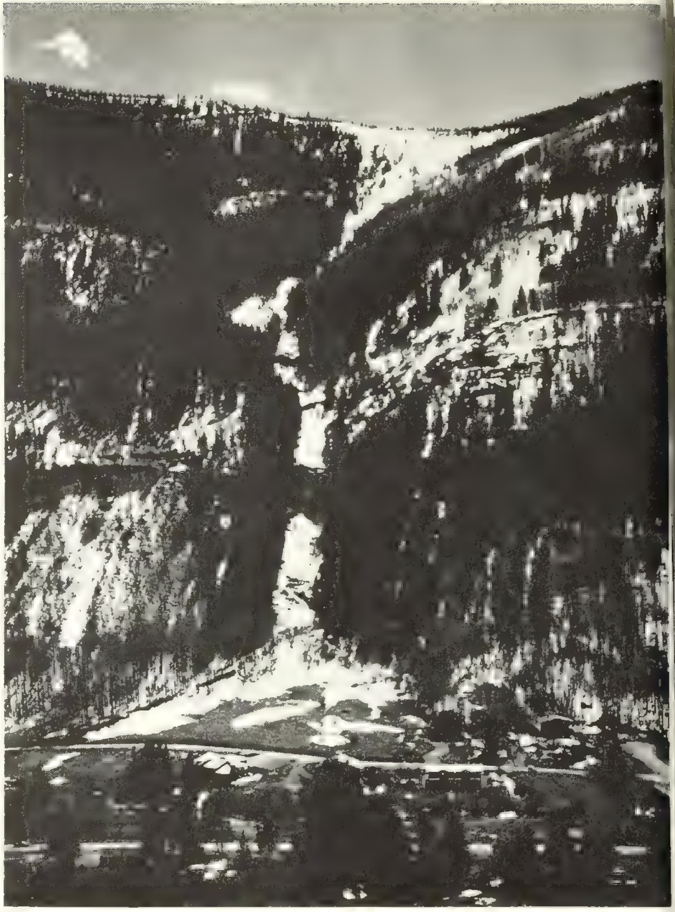


Figure 12.—Cliff bands in the track of this avalanche path can transform moderately large, flowing avalanches into powder avalanches because of entrainment of air into the flow. (Waterfall Avalanche, Vail, Colo.)

Table 2.—Some powder avalanche characteristics

Size classification	Velocity range	Bulk density	Flow height
	m/s	*kg/m³*	*m*
Moderate	50–70	2–20	5–10
Large	70–100	2–20	10–20

A fully developed powder avalanche usually moves at velocities exceeding 30 m/s and probably has a bulk density in the range of 2-20 kg/m³. Powder avalanche flow depth should be assumed to exceed 10 m, a depth sufficient to envelope an average sized, single-family dwelling. Because of this large flow depth and velocity, powder avalanches produce forces similar to those of a windgust of increased density. When a powder avalanche engulfs an object, a reference pressure, called the stagnation pressure, at the upstream face of the object can be computed by assuming $K = 0.5$ (eq. [11]). Stagnation pressure P_s is equal to

$$P_s = 1/2\ \rho' V^2 \qquad [12]$$

It must be remembered that P_s is only a reference pressure. To compute the design unit forces and total aerodynamic force on an object, P_s must be multiplied by the exposed area and by a coefficient of drag or lift. The total drag force F_d acts on the object in a direction parallel to the flow and is calculated

$$F_d = C_d A_d\,(1/2\ \rho' V^2) \qquad [13]$$

where A_d is the projected area normal to the flow and C_d is a coefficient which must be determined in-

---

[3] *Density ρ' has the units of mass/volume. In the SI system of units ρ' has the dimensions kg/m³. The unit weight, γ, is computed $\rho' g$ (kg/m² s²).*

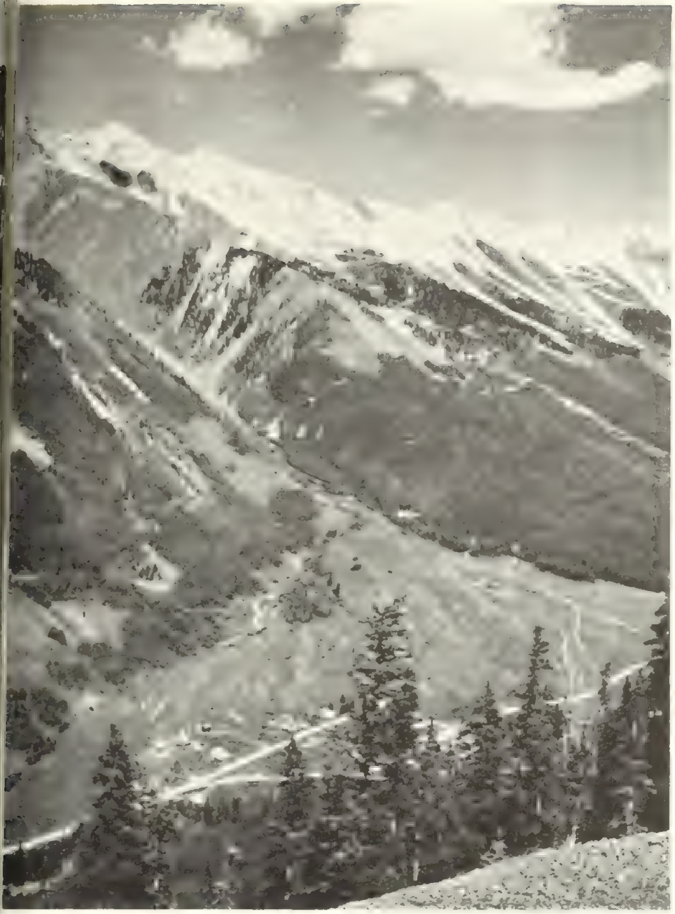


Figure 13.—This avalanche discharge onto an alluvial fan. Wet slides in particular are deflected by ridges and gullies on the fan surface and can take unpredictable paths in the runout zone. However, dry-snow and powder avalanches tend to run directly across the fan. (Spring Gulch Avalanche, San Juan Mountains, Colo., photograph by Doug Wolfe of Ophir, Colo.)

dividually through an aerodynamic analysis of the structure. Aerodynamic studies show that, for large objects subject to loading from high velocity winds or powder avalanches, $0.5 < C_d < 1.5$. This range of values is only a rough estimate, but does indicate the wide range of values applicable to real structures.

The lift force F_1 is calculated

$$F_1 = C_1 A_1 \left(1/2\ \rho' V^2\right) \qquad [14]$$

where C_1 is the coefficient of lift. This coefficient must also be determined by an aerodynamic analysis of the structure. Generally, $C_1 < C_d$ for most structures which must be designed for the impact of powder avalanches. The area A_1 is the projection of the area of the impacted object on a plane parallel to the flow.

Numerical Example.—The design powder avalanche will be at least 15 m deep at the location of the building. Computations (see Design Criteria section) suggest that $V = 40$ m/s. Density is assumed equal to 10 kg/m³ throughout the depth of the powder avalanche. Application of equation [12] enables computation of a stagnation pressure

$$P_s = (1/2)(10)(40^2) = 8{,}000\ \text{kg/m}^2\text{s}^2 = 8{,}000\ \text{N/m}^2$$
$$= 816\ \text{kg(wt)/m}^2 = 167\ \text{lb/ft}^2$$

If it is known that the building will have an area normal to the flow A_d equal to 18 m², and C_d is 1.2, as determined by an aerodynamic study of the particular structure, then application of equation [13] gives a total normal force

$$F_d = (1.2)(18)(8{,}000) = 172{,}800\ \text{N} = 17{,}630\ \text{kg} = 38{,}880\ \text{lb}$$

If it is also known that the projected roof area A_1 equals 30 m² and C_1 is determined to be 0.5, equation [14] gives

$$F_1 = (0.5)(30)(8{,}000) = 120{,}000\ \text{N} = 12{,}240\ \text{kg} = 27{,}000\ \text{lb}$$

The magnitude of the resultant force acting on the building from powder avalanche loading is shown in figure 14. The resultant force F and the angle through which it acts is calculated by vector addition of F_1 and F_d.

The methods described here to compute forces from powder-avalanche loading do not differ from methods used to compute wind loads. Thus, engineering methods used in building design for wind loading can be freely applied in design for powder avalanches. It should be remembered that the effective bulk density of the avalanche "fluid" may be from 2 to 20 times greater than clear air density. This example assumes steady flow around the object.

Dense Flowing Avalanche Impact

When a dense mass of flowing snow impacts an object, the flow is either deflected by the object or is brought to rest against it, suffering nonrecoverable deformation and increasing the bulk density of the flowing snow to some much higher density.

If all of the snow is deflected laterally by the object, deposition and compression of snow do not occur at the object and the direction of the flow is changed by 90°.

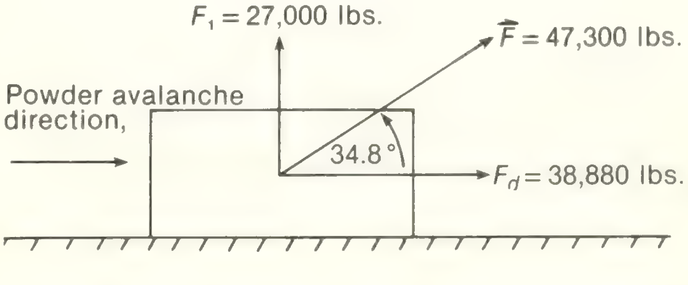


Figure 14.—Resultant force acting on a building from powder avalanche loading.

In this case, the value of K in equation [11] is 1.0, and the expression for dynamic pressure becomes

$$P = \rho' V^2 \qquad [15]$$

However, the snow from dry avalanches is typically compressed against objects to densities of 300-550 kg/m^3, several times the mean bulk densities of the avalanche before impact. According to Mellor (1968), the effect of density increases upon impact can be accounted for by assuming snow behaves as a compressible plastic material. Compressibility effects are considered by assuming $K = \rho_2/(\rho_2 - \rho')$ where ρ' and ρ_2 are the respective densities before and after impact. If we assume, as a typical value, that $\rho_2 = 3\rho'$, then K equals 1.5 and the expression for dynamic pressure becomes

$$P = 1.5\rho' V^2 \qquad [16]$$

Equation [16] should be used to compute impact pressures of flowing avalanches against large, flat surfaces.

Mixed Motion Avalanche Impact

Some structures are reached by both flowing and powder avalanches during separate events or during the same event. When this is the case, designers must consider both types of impact.

DEFLECTING AND GUIDING STRUCTURES

Introduction and Terrain Considerations

Deflecting structures are intended to change the direction of flowing avalanches, thereby limiting the area of the natural runout zone. Powder avalanches are generally too deep and are of too high a velocity to be deflected; they tend to override deflecting structures. Deflecting structures have proven to be most useful in cases where an avalanche confined to a gully discharges onto an alluvial fan at the base of the gully. In such cases, uncontrolled dry-snow avalanches would tend to spread laterally across the fan. Wet-snow avalanches may assume a digitate form on an alluvial fan as each advancing finger of snow is deflected to new directions by small-scale terrain irregularities (fig. 7). An example of a broad alluvial fan upon which avalanches are known to have spread for long distances is shown in figure 13.

Although large areas can be made relatively hazard-free by carefully designed and located deflecting structures, it is necessary that planners identify the most desirable locations for the protected objects. It is possible that the runout distance may actually be increased in the direction to which the snow is deflected because the avalanche flow depth may be increased in the direction of the deflection.

Guiding and deflecting structures will be most effective on runout zone and lower-track slopes of 12-20°. On slopes steeper than 20°, dry, flowing avalanches of design size may flow at high velocities and tend to override deflecting structures. In contrast, on slopes less than approximately 12°, even large avalanches tend to deposit much of their mass. Deposition of snow against a structure reduces its effectiveness because such deposition reduces the effective height of the structure. Deposition and overtopping are serious design problems with all structures located in the lower track and runout zone including catching, retarding, and direct-protection structures. No clearcut guidelines can be given as to the optimum steepness of terrain upon which structures should be placed. The small design avalanches typical of small paths (fig. 1), will begin to decelerate and deposit debris on steeper slopes, perhaps of 15-25°. In such cases, because of lower maximum velocities, it may be possible to deflect the flow on slopes steeper than 20°. In contrast, very large design avalanches on major paths may only begin to decelerate and deposit on slopes of less than 15° (fig. 3). Thus, design-avalanche parameters must be calculated as discussed in the section on Design Criteria before defenses can be located or sized, and the expected area of avalanche deposition must be determined.

If avalanches smaller than design size frequently deposit debris against structures, it may be necessary to clean debris away periodically in order to maintain the effectiveness of the structure.

In figure 15, confined and unconfined avalanche paths are compared in terms of suitability for deflection of avalanches. It can be seen that a much greater, relative area can be protected in a confined avalanche path.

Design Height of Guiding Structures

Guiding structures are not intended to change avalanche direction, but to prevent an avalanche from spreading laterally. The required height of guiding structures depends on the flow height, cross-sectional area, and hydraulic radius of the natural avalanche. Computation of guiding-wall height is illustrated in figure 16.

Numerical Example.—(Explanation for figure 16).

Avalanche conditions:

The natural channel has a slope of 25°, a flow height of 10 m, side slopes of 45°, and cross section area of 100 m^2. The guide channel has a slope of 15° and a width of 20 m. Guide channel height is unknown and must be calculated. Assume coefficient of sliding friction to be 0.20.

To compute guide wall height apply the continuity equation,

$$R_l F_l^2 = \frac{(\sin \alpha_u - \mu \cos \alpha_u)}{(\sin \alpha_l - \mu \cos \alpha_l)} R_u F_u^2$$

where R_u and R_1 are the hydraulic radius of the upper and lower channels, respectively; F_u and F_1 are the cross-sectional areas of upper and lower channels,

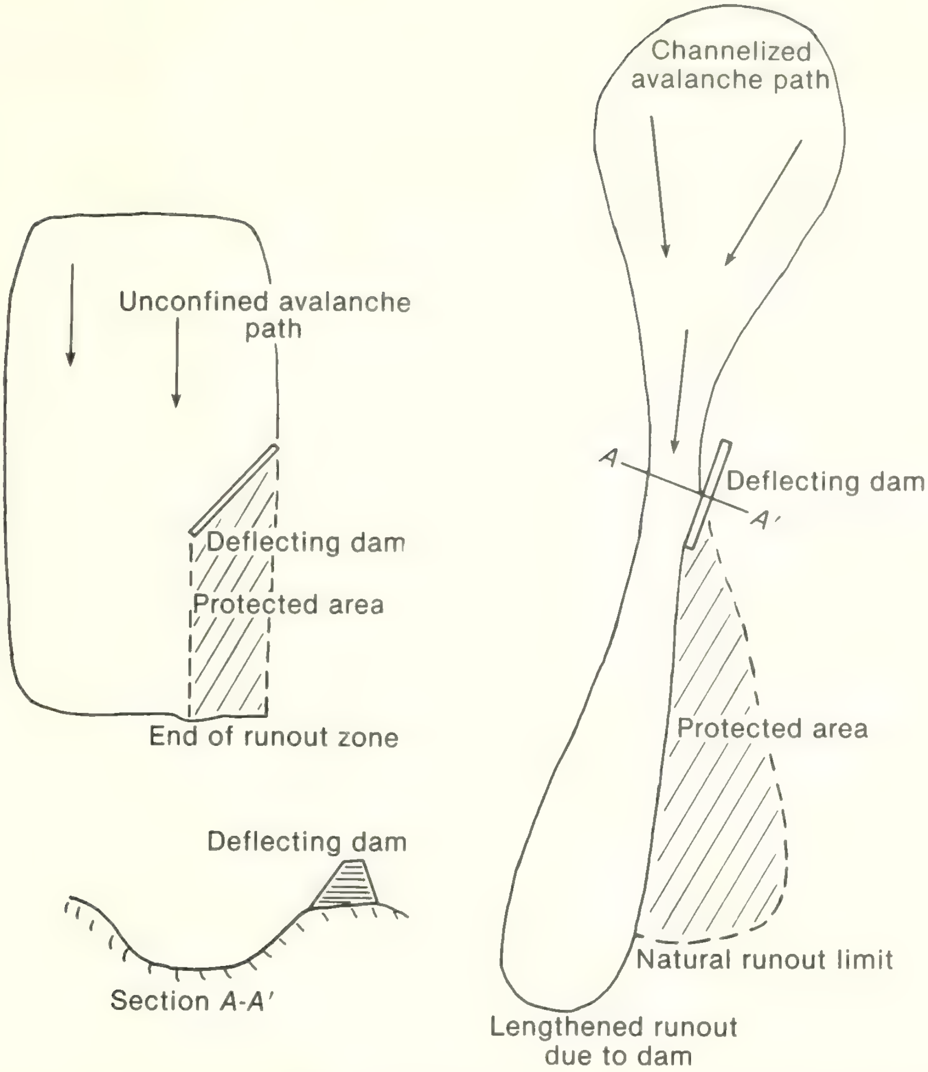


Figure 15.—Illustration of the relative effectiveness of two deflecting dams of comparable length. The dam protects a smaller area below the unconfined path. The runout zone may be lengthened as a result of deflecting the flow.

respectively; α_u and α_l are the slopes of the upper and lower channels, respectively; and μ is the coefficient of sliding friction.

Because the guiding channel is rectangular,

$$R_l F_l^2 = \frac{20h'}{2h'+20}(20h')^2$$

Thus,

$$\frac{(8{,}000h'^3)}{2h'+20} = \frac{(\sin 25^\circ - .2\cos 25^\circ)}{(\sin 15^\circ - .2\cos 15^\circ)}(R_u F_u^2) = 130{,}300$$

Solution of the above equation yields $h' = 8.4$ m, the required height of the guiding walls. Note that the hydraulic radius is equal to the channel cross-sectional area divided by the wetted perimeter.

Design of Deflecting Structures

Design alternatives consist of straight or curved structures. Either may consist of earthen dams or structural dams designed for impact. The choice of structure type depends on the shape of natural terrain irregularities and the availability of materials.

Straight Deflecting Walls

When the momentum of an avalanche is changed, as by altering the flow direction with a deflecting wall, the flow depth will increase at the object. This flow-depth increase is the climbing height h which is a function of velocity V, deflecting angle ϕ, and acceleration of gravity g. The design height H of the structure is the sum of climbing height h, flow height h', and snowpack depth h_0. These quantities are illustrated in figure 17. Design height H is computed by

$$H = h_0 + h' + h \qquad [17]$$

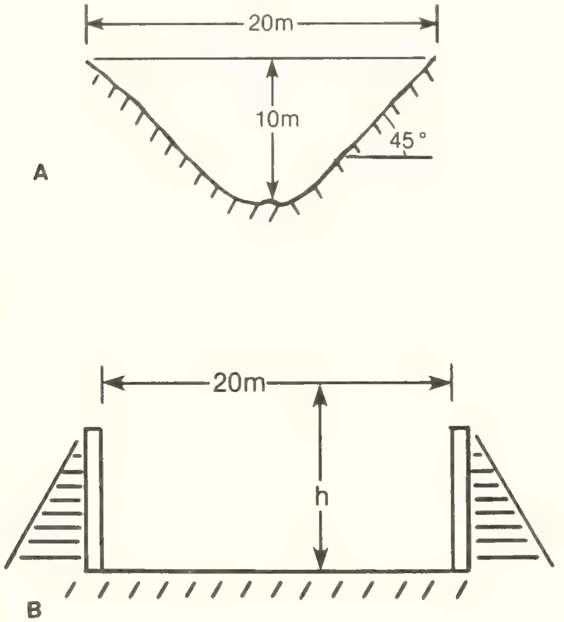
Climbing height is calculated as $h = (V \sin \phi)^2/2g$. Thus, equation [17] becomes

$$H = h_0 + h' + (V \sin \phi)^2/2g \qquad [18]$$

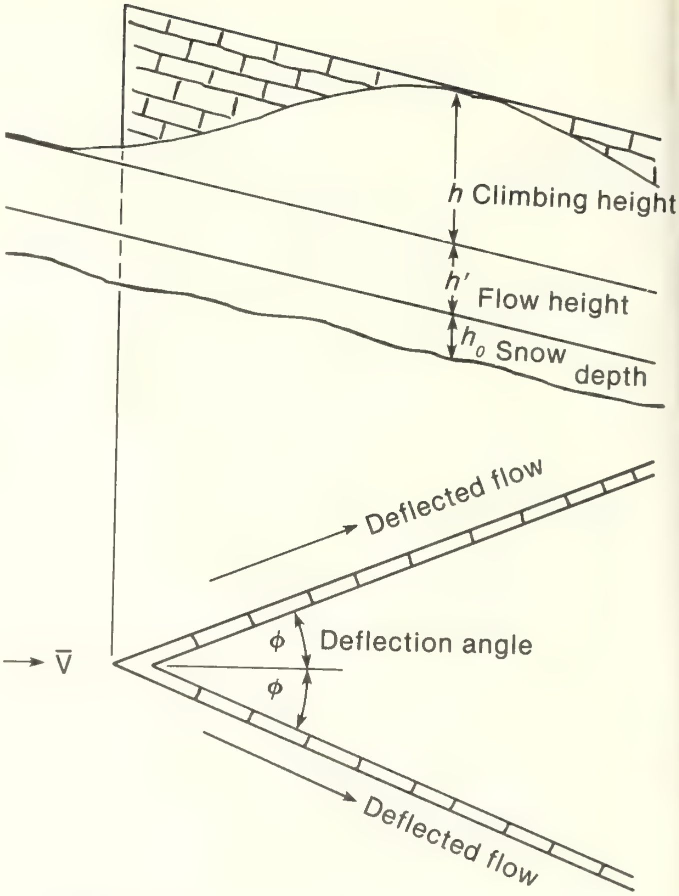
When ϕ is zero, there is no deflection and the wall behaves as a guiding wall. If ϕ equals 90°, the wall acts as a dam or a catching structure.

The design height increases rapidly with both velocity and deflecting angle; consequently, it is often recommended that ϕ be kept as small as possible. Consider, for example, a design avalanche with the following characteristics: $V = 25$ m/s, $h' = 2.0$ m, $h_0 = 1.0$ m, and $\phi = 15°$. In this case, $H = 4.74$ m, but if ϕ is increased to 30°, then H increases to 10.97 m.

Deflection forces result when the momentum of an avalanche is changed by an object. The following discussion of deflection forces is applicable to vertical structural walls and to the splitting-wedge type of direction-protection structure (discussed further in the section on Direct Protection Structures). Earthen structures need not be designed for deflecting forces because of their large mass. The magnitude of the deflection force depends on the avalanche velocity and density, the deflection angle ϕ and the area of the impact surface. These quantities are illustrated in figure 18.



Figures 16.—Dimensions of guiding structure. (A) Natural avalanche channel above guiding structure, (B) Cross section view of guiding structure.



Figures 17.—Design height of a deflection wall (or wedge). Design height, $H = h_0 + h' + h$.

The specific deflection force (i.e., the force per unit area of impacted surface) can be defined in terms of three mutually perpendicular components: normal, shear, and uplift. In the view of the uncertainties that exist regarding the details of avalanche impact (see Avalanche Impact section), it should be assumed that $0.5P_n = P_s = P_v$, where P_n is the normal pressure, P_s is shear, and P_v is uplift. The normal pressure P_n is calculated as

$$P_n = \rho'(V \sin \phi)^2 \qquad [19]$$

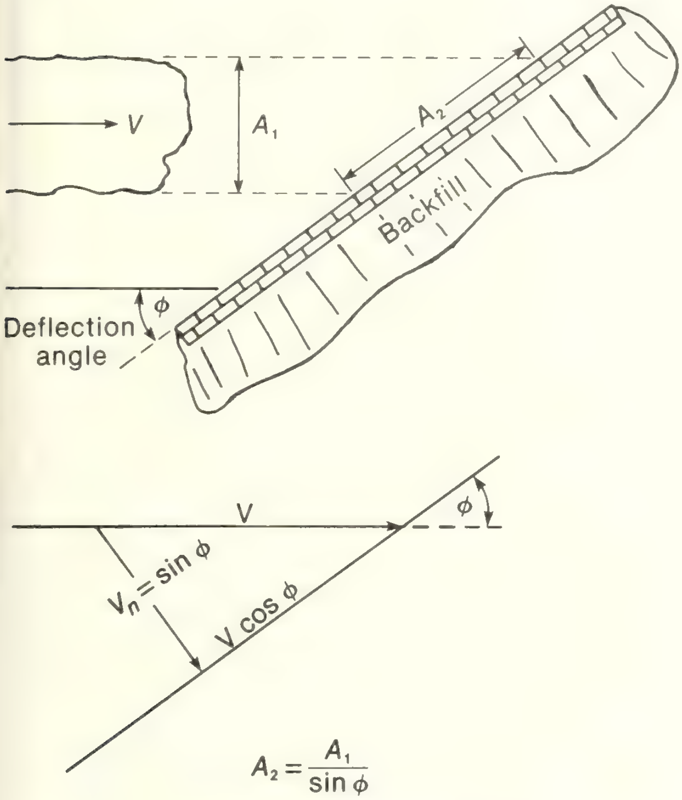
where ρ' is the avalanche density. Thus, for $\phi = 90°$, $P_n = \rho' V^2$, the expression for fluid impact on a large, flat surface normal to the flow direction.

The total dynamic force on a wall is equal to the summation of all specific deflection forces times the areas over which these specific forces act. As illustrated in figure 18, an entire wall will not be affected by impact because some finite distance is required before the avalanche can reach maximum height. Because this distance is unknown, it should be assumed that the impact area is equal to the design height times the length of the wall.

The total normal force F_n per unit length of wall is

$$F_n = P_n H + \rho g H^2/2 \qquad [20]$$

where $\rho g H^2/2$ is the "hydrostatic" force per unit length of wall. This expression for "hydrostatic" force is an overestimate because it does not take the shear strength of the snow into account, but, because shear strength varies considerably and cannot be estimated in advance, the simple expression given in equation [20], which assumes zero shear strength, should be used in design. Figure 19 illustrates the locations of resultants of the dynamic and static normal forces on a flat, vertical wall.



$$A_2 = \frac{A_1}{\sin\phi}$$

Normal Pressure: $\rho' V_n^2$

$$P_n = \rho'(V \ \sin\phi)^2$$

Deflection force:

$$F^2 = P_n A_2 = \frac{\rho' V_2 \sin^2\phi \, A_1}{\sin\phi}$$
$$= (\rho' V^2 \sin\phi) A_1$$

Shear: $P_n \mu$

Figures 18.—Deflection wall: forces and unit forces. V = Avalanche velocity, A_1 = Cross-section of avalanche front, A_2 = Area or impact surface on wall.

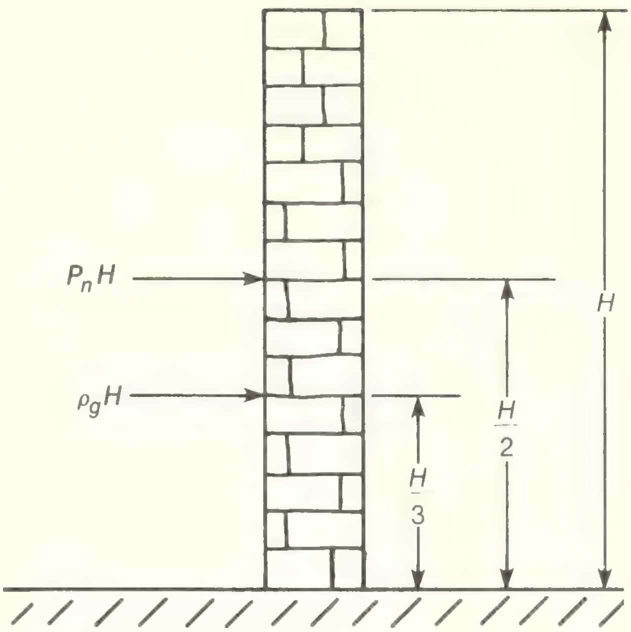


Figure 19.—The location of the resultants of the normal forces on a flat, vertical wall.

Numerical Example.—Compute the forces acting per unit length on a wall deviating 30° from the avalanche flow direction ($\phi = 30°$). The design-avalanche characteristics at the wall location are: $V = 20$ m/s, $\rho' = 200$ kg/m³, and $h' = 1.0$ m. The snowpack depth, h_0, can be assumed to be 0.5 m.

From equation [18],

$$H = 0.5 + 1.0 + 20(0.5)^2/19.6 = 6.6 \text{ m}$$

thus, the required wall height is 6.6 m. The normal pressure from equation [19] is

$$P_n = 200[(20)(0.5)]^2 = 20{,}000 \text{ N/m}^2$$

and $P_v = P_s = 10{,}000$ N/m². The average "hydrostatic" force per unit length of structure is

$$\rho g H^2/2 = \frac{200(9.8)(6.6)^2}{2} = 42{,}700 \text{ N/m}$$

thus, the total normal force per unit length (eq. [20]) of structure wall equals

$$F_n = P_n H + \rho g H^2/2 = 20{,}000(6.6) + 42{,}700 = 175{,}000 \text{ N/m}$$
$$= 17{,}800 \text{ kg/m} = 12{,}000 \text{ lb/ft}$$

$$F_v = (P_n/2)H = 10{,}000(6.6) = 66{,}000 \text{ N/m}$$
$$= 6{,}730 \text{ kg/m} = 4{,}530 \text{ lb/ft}$$

$$F_s = (P_n/2)H = 10{,}000(6.6) = 66{,}000 \text{ N/m}$$
$$= 6{,}730 \text{ kg/m} = 4{,}530 \text{ lb/ft}$$

Curved Deflecting Walls

A curved deflecting wall is desirable in cases where it is necessary to gradually change the direction of an avalanche. In some cases, such as near the top of some alluvial fans, the natural terrain irregularities, including channels and debris-flow levees, may favor this type of construction.

The design height of a curved wall, as with a straight wall, is computed as

$$H = h_0 + h' + h$$

where all terms are defined as in equation [17]. However, for the curved wall, the climbing height, $h, = V^2W/gR$ and the equation becomes

$$H = h_0 + h' + \frac{V^2W}{gR} \qquad [21]$$

where W is the width of the avalanche in the artificially curved section of the channel and R is the radius of curvature of this section. These quantities are further illustrated in figure 20.

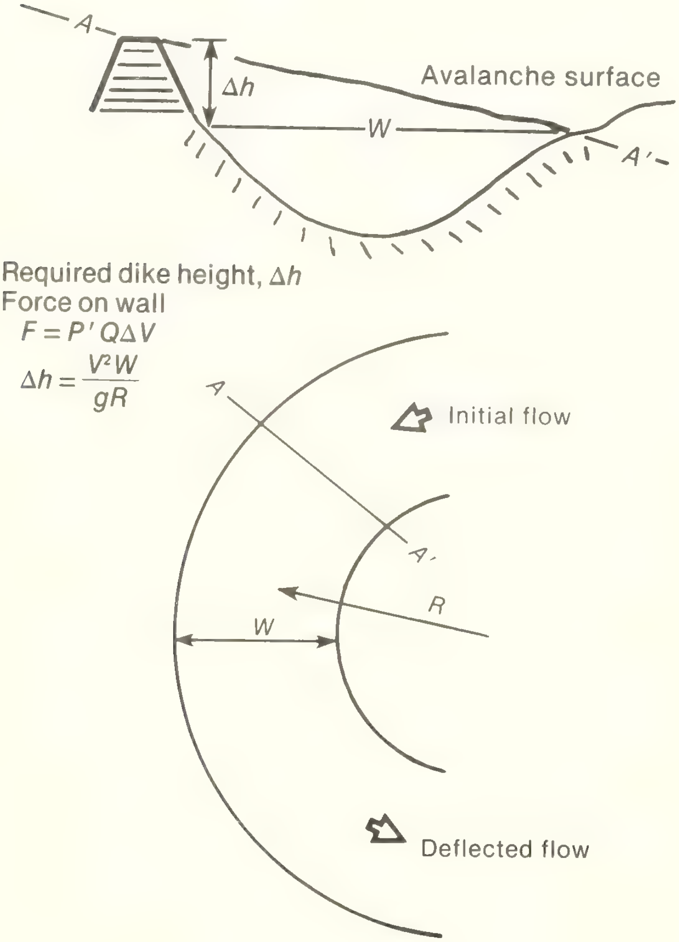


Figure 20.—Nomenclature and parameters needed to calculate dimensions of a curved deflecting wall.

The magnitude and direction of dynamic forces on the curved deflecting-wall surface are illustrated in figure 21, where the quantity Q is the design-avalanche discharge (see Design Criteria section for a discussion of Q). The x and y components of the dynamic deflection force F_x and F_y are computed based on a coordinant system as shown in figure 21. The deflection force F is equal to the vector addition of F_x and F_y, thus,

$$\overline{F} = (F_x^2 + F_y^2)^{1/2} \qquad [22]$$

where

$$F_x = \rho' Q(V_{2_x} - V_{1_x}) \qquad [23]$$

and

$$F_y = \rho' Q(V_{2_y} - V_{1_y}) \qquad [24]$$

The various velocity components used in these calculations are defined in terms of the initial avalanche velocity as it reaches the deflecting structure V_1, and the velocity as the avalanche leaves the structure V_2. For practical purposes, it may be assumed that V_1 equals V_2 whenever the wall length is short compared to the runout distance. The velocity components are defined as

$$V_{2_x} = V_1 \cos \delta$$

$$V_{1_x} = V_1 \cos 0° = V_1$$

$$V_{2_y} = V_2 \sin \delta$$

$$V_{1_y} = V_1 \sin 0° = 0$$

The angle δ, as defined in figure 21, is equal to the maximum change in the avalanche flow direction as a result of deflection by the curved wall.

It should be remembered that these equations are borrowed directly from fluid dynamics and assume the snow avalanche is a moving field. Forces are computed by calculating momentum change in a fluid. In a real avalanche, we may expect the behavior to differ from that of a true fluid at the structure. Frictional forces are activated upon impact and snow will tend to be deposited against the structure. The discharge Q, therefore, will decrease with distance along the structure, especially if the structure is located near the bottom of the runout zone in an area of low gradient. As discussed previously, the meaning of low gradient varies for avalanche sizes and types.

In addition to the dynamic forces illustrated and discussed, a normal "hydrostatic" force also exists and is equal to

$$\left(\frac{\rho g H^2}{2}\right) L \qquad [25]$$

where L is the length of the wall. The total force on the curved wall surface is equal to the vector summation of the hydrostatic force and the dynamic deflection force.

Numerical Example.—Compute the resultant dynam- force and the 'hydrostatic" force on a curved deflect- g wall surface. The design avalanche characteristics t the structure are: $V_1 = 25$ m/s, $W = 10$ m, $h_0 = 0.5$ m, $' = 2.0$ m, $\rho = 200$ kg/m³, and $Q = 1{,}000$ m³/s. The deflec- on wall has a radius of curvature R of 100 m; $\delta = 20°$.

From equation [21], the design height is

$$H = 0.5 + 2.0 + 6.25 = 8.7 \text{ m}$$

he dynamic force (fig. 21 and eq. [22]) equals

$$\begin{aligned}\overline{F} = \{ &[200{,}000(25 \cos 20° - 25)]^2 \\ &+ [200{,}000(25 \sin 20° - 0)]^2\}^{1/2} \\ &= 1{,}740{,}000 \text{ N} = 177{,}000 \text{ kg} = 391{,}000 \text{ lb}\end{aligned}$$

he "hydrostatic" force, from equation [25], equals

$$\begin{aligned}\frac{200(9.8)(8.75)^2}{2}\, 34.9 &= 2{,}619{,}000 \text{ N} \\ &= 267{,}200 \text{ kg} = 589{,}200 \text{ lb}\end{aligned}$$

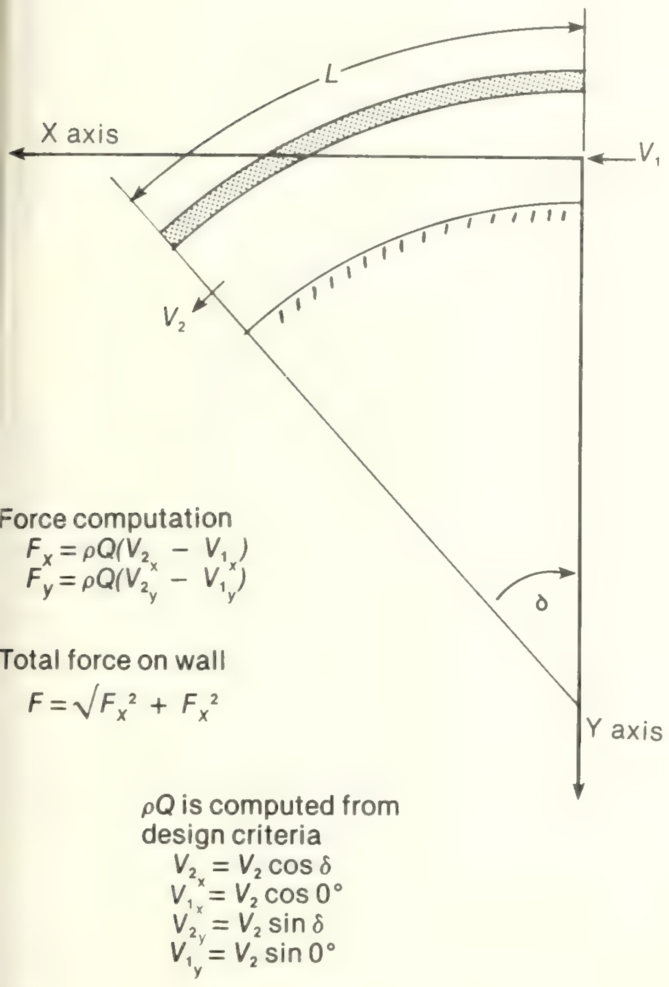

L
X axis
V_1
V_2
δ
Y axis
Force computation
$F_x = \rho Q(V_{2_x} - V_{1_x})$
$F_y = \rho Q(V_{2_y} - V_{1_y})$
Total force on wall
$F = \sqrt{F_x^2 + F_x^2}$
ρQ is computed from design criteria
$V_{2_x} = V_2 \cos \delta$
$V_{1_x} = V_2 \cos 0°$
$V_{2_y} = V_2 \sin \delta$
$V_{1_y} = V_2 \sin 0°$

Figure 21.—Computation of total force on a wall.

Wall length L is computed as

$$L = (\delta/360)(2\pi R) \qquad [26]$$

Therefore, in this example,

$$L = (20/360)[(2)(3.14)(100)] = 34.9 \text{ m}$$

Volume and Cost of Earthen Deflecting Walls

It will often be true that earthen deflecting walls will be more economical than structural walls. The cost of earthen walls is mainly a function of the amount of unconsolidated material that must be moved during construction; thus, it is important to be able to relate wall volume required to protect a given area to the deflection angle. It is recognized that the same area can be protected by a short, high wall with a high deflection angle as can be protected by a long, low wall using a low deflection angle, but space available is usually the principal consideration.

Dimensional analysis shows that, for a given width of protected area and a given avalanche velocity at the defense structure, the required earthen structure volume increases in proportion to $(\sin \phi)^3$. The relative volume of a structure is shown as a function of ϕ in figure 22. Figure 22 demonstrates the sensitivity of volume to deflection angle, especially in the range of $20° \leqslant \phi \leqslant 50°$. For example, an increase in ϕ from 30° to 50° requires a 3.5-fold increase in wall volume.

CATCHING STRUCTURES

Purpose

Catching structures are intended to stop flowing avalanches and the lower portions of mixed motion and powder avalanches, thereby defining the lower limit of the design avalanche. Where mixed motion and powder avalanches are the design case, it may be possible to stop most of the avalanche mass behind a catching structure, allowing the more diffuse, low-density, powder portion to overtop the structure and continue into the runout zone. If powder avalanches are expected to continue into the runout zone, exposed structures below the catching structure should be designed for powder avalanche impact (see sections on Avalanche Impact and Direct Protection Structures). There is a possibility that a powder avalanche will be deflected upward by a catching structure, causing the impact to be down upon the top of exposed structures farther into the runout zone. This possibility should be carefully avoided through design.

As subsequent discussion will show, it is not practical to completely stop high-velocity avalanches regardless of the type. Thus, avalanche velocity and flow height are the controlling factors in assessing design feasibility and must be determined prior to design, as discussed in the Design Criteria section.

Terrain Considerations

Field observations of avalanche-debris distribution suggest that large avalanches begin to deposit debris and decelerate on slopes of less than 15-20°. Thus, catching structures will generally be more effective on slopes of less than 20° where avalanches lose energy naturally. If the design avalanche has very high velocity and great flow height, catching structures should be placed only on slopes of less than 15°. These reduced slopes are found not only in most runout zones but also higher in the avalanche track at breaks in slope.

Construction of catching structures in the track must be approached with caution. Construction locations often may be reached by small to medium sized avalanches of much less than design size. If this happens often enough during a given winter, catching structures may become backfilled with snow and their effectiveness will be reduced because the effective height of the structure will become less. If small slides are frequent enough, the structures intended to stop large avalanches may become completely filled with snow and can serve as ramps off of which high-velocity avalanches may become airborne. This could increase the runout-zone length.

If the runout zone is long and of moderate gradient, large avalanches will decelerate gradually. Catching dams should be located far into the runout zone where reduced velocity is anticipated and where smaller avalanches seldom penetrate.

Structure height can be determined given the design-avalanche velocity V, flow height h' and the snowpack depth at the structure h_0. The design height H of a vertical structure is determined from the expression

$$H = h_0 + h' + V^2/2g \qquad [27]$$

where g is the gravitational acceleration. Equation [27] is very sensitive to avalanche velocity and provides an upper limit for design height. For earthen structures with side slopes of θ degrees, the expression for design height becomes

$$H = h_0 + h' + V^2/2g(1 + \mu \cot \theta) \qquad [28]$$

where μ is the coefficient of friction between the avalanche and the structure. Assuming $\mu = 0.4$ and side slopes of 1.5:1 ($\theta = 33.7°$), equation [28] becomes

$$H = h_0 + h' + V^2/3.2g \qquad [29]$$

Equations [28] and [29] give smaller estimates of H than equation [27] because it is assumed that some of the avalanche energy is consumed as frictional work as the avalanche slides up the sloping face of the catching dam. Application of equation [29] shows how the required dam height becomes very large even for moderate avalanche velocities. For example, when $h_0 = 1.0$ m, $h' = 1.5$ m, and $V = 20$ m/s, the design height from equation [29] is 15.2 m. This shows quantitatively why it is impractical to stop large, fast-moving avalanches with a catching dam (figs. 23, 24).

The forces on a vertical, structural catching dam can be calculated by the methods given in the section on Avalanche Impact. It should be assumed that all of the snow is either stopped or is deflected through 90°; thus, the expression for normal pressure applies and $P_n = \rho' V^2$. Uplift forces will also occur against the wall and is manifested as vertical shear P_v per unit area. P_v should be assumed equal to $0.5P_n$.

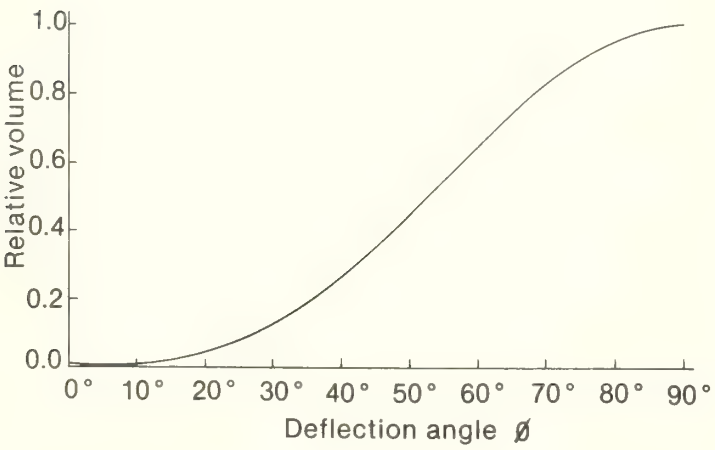


Figure 22.—Volume as a function of deflecting angle for an earthen dam. (Assumes volume is proportional to sin ϕ^3.)

Snow Storage Volume

Regardless of the adequacy of dam height, sufficient storage volume for the compressed avalanche snow must be provided behind the dam (fig. 25). If sufficient storage volume is not provided, avalanches can quickly fill in behind the dam. The mass of snow deposited behind the dam in a single design-avalanche event should be assumed equal to the mass released in the starting zone during the design avalanche (see Design Criteria section). It should also be assumed that $\rho_1 = 2\rho_0$, where ρ_1 equals the mean density of the avalanche deposit, and ρ_0 equals the mean density of the snowpack involved in the design avalanche. Thus, a maximum estimate of the necessary snow-storage volume is equal to half the volume of the starting zone. This is an overestimate because some of the avalanching snow will be deposited in the track above the catching structure.

However, as previously discussed, more than one avalanche may reach the storage area during a single winter, requiring that additional volume be provided for storage. The past history of avalanches at a given site must be determined in order to estimate avalanche frequency and to assess the reliability of a catching structure.

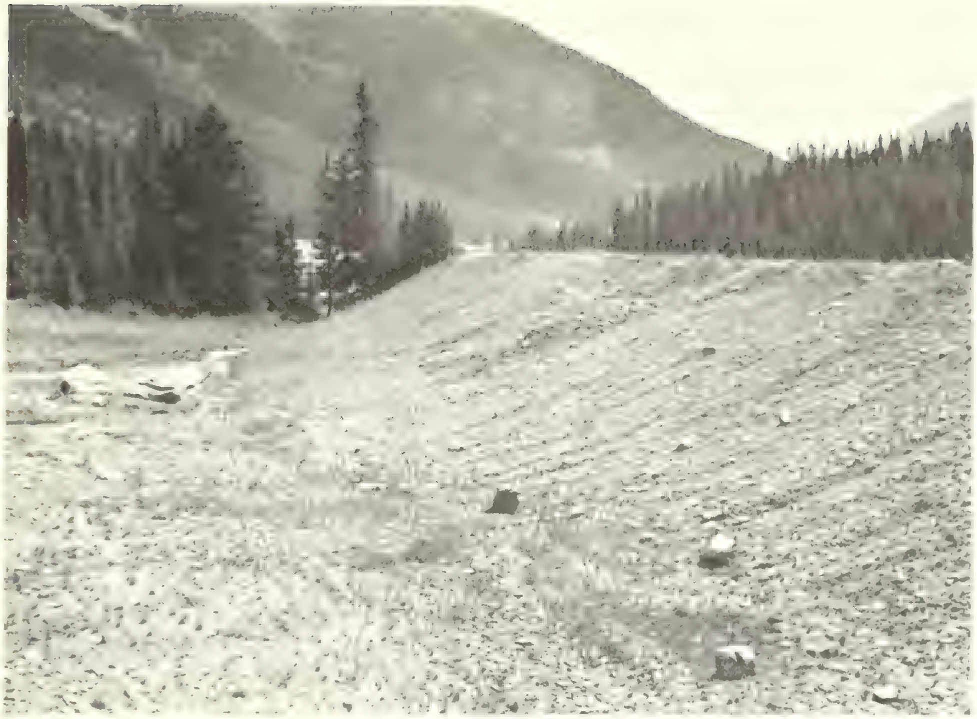


Figure 23.—This catching dam is built perpendicular to the flow of a large avalanche but is only 5 m high. An avalanche moving only 10-15 m/s would be able to overtop this structure. (Bethel Avalanche, near Silver Plume, Colo.)

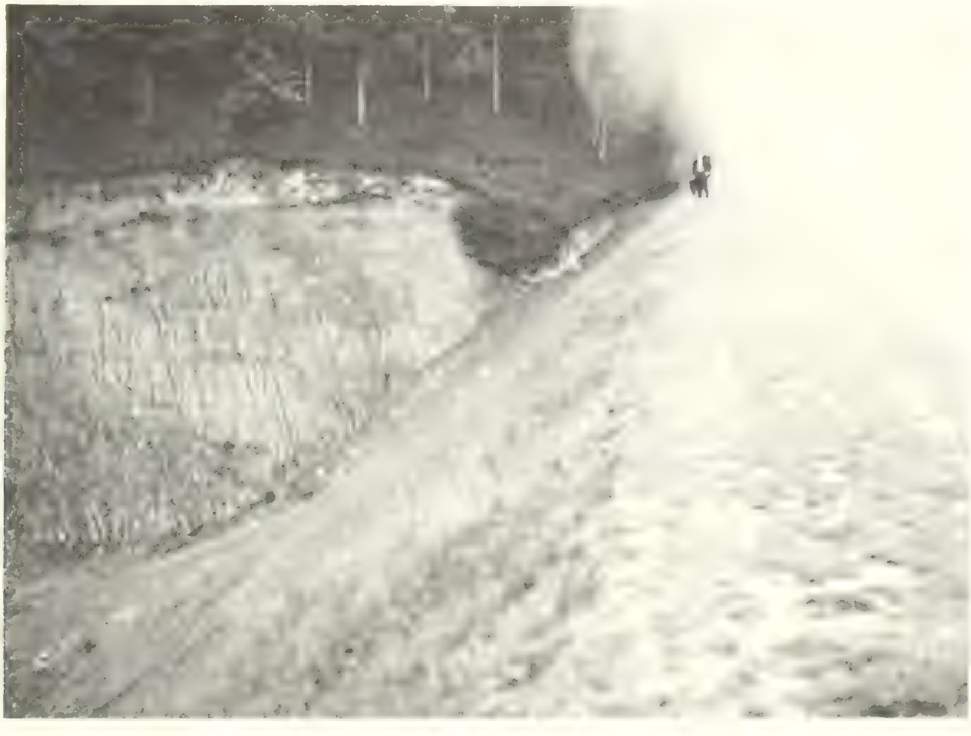


Figure 24.—This catching dam is 20 m high and, according to equation [28], will stop an avalanche with a velocity of 22-25 m/s. Sufficient snow-storage volume is provided to stop a large avalanche. In spite of the large size of this catching dam, design engineers recognize that large, powder avalanches will easily overtop the dam. However, the nearest buildings are 500 m farther into the runout zone. (Innsbruck, Austria)

Reduction of Velocity and Length of Runout Zone

The forward velocity of an avalanche will be reduced even if the dam is overtopped because some of the kinetic energy of the avalanche is consumed in climbing the dam (fig. 23). It may be assumed that an equivalent amount of energy is not regained as the avalanche descends the downhill side of the dam because, in general, the downhill slope of the dam face will not be long enough or steep enough to permit significant acceleration of the avalanche.

The velocity reduction ΔV may be computed

$$\Delta V = [2g(H - h_0)(1 + \mu \cot \theta)]^{1/2} \qquad [30]$$

where H equals dam height, h_0 equals snowpack height (or height of previous avalanche deposits), μ equals the coefficient of friction between the avalanche and the dam, and θ equals the slope angle of the dam face. Assuming μ equals 0.4, and a side slope of 1.5:1 ($\theta = 33.7°$) for an earth-filled dam, equation [30] simplifies to

$$\Delta V = \sqrt{3.2g(H - h_0)} \qquad [31]$$

Calculation according to equations [30] or [31] enables a readjustment of the computed avalanche runout distance by use of equations [3] or [4]. The avalanche flow height may not be reduced even though velocity reduction takes place.

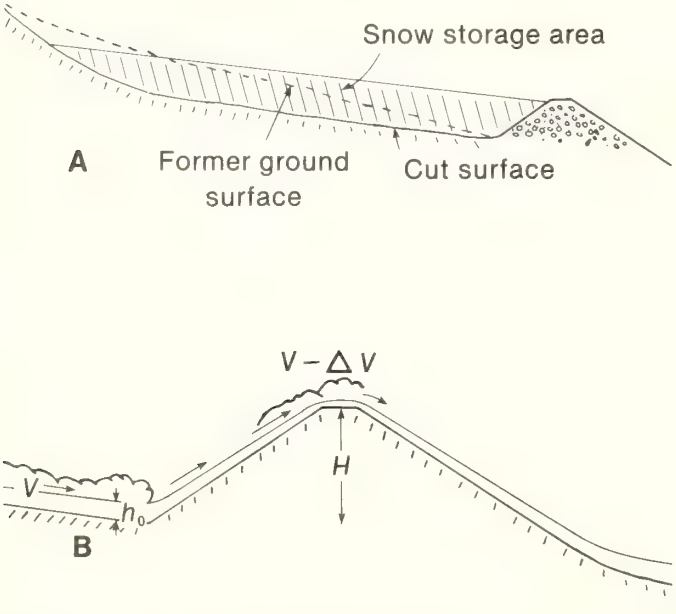


Figure 25.—Catching dams should be placed on slopes with gradients of less than 15-20° for maximum effectiveness. Sufficient storage volume should be provided to accommodate the debris from the design avalanche. (A) Relationship of dam to snow storage area, (B) Design height and velocity reduction.

Numerical Example.—A design avalanche has a computed velocity of 25 m/s and a flow height of 2.0 m. The snowpack depth is 1.0 m. A catching dam 10 m high with 1-1/2:1 side slopes is placed across the flow jus above a runout zone of 8° inclination. It is assumed that μ equals 0.4 on the dam face. What will be the reduction in velocity and runout distance as a result of the dam?

From equation [31], the velocity reduction is

$$\Delta V = \sqrt{(3.2)(9.8)(10 - 1)} = 16.8 \text{ m/s}$$

Therefore, the adjusted velocity below the dam becomes

$$V - \Delta V = 25 - 16.8 = 8.2 \text{ m/s}$$

The runout distance reduction is computed by use of equation [3]. Assuming $\xi = 600$ m/s² and $\mu = 0.2$ in both cases, and assuming a velocity of 25 m/s without the dam and 8.2 m/s below the dam, the runout distances are as tabulated below.

	Velocity	Runout distance
With dam	8.2 m/s	39 m
Without dam	25 m/s	100 m

Thus, the runout distance can be shortened by 61 m. The volume of avalanche debris deposited below the catching dam will be reduced approximately by the volume stored above the dam.

Again, very deep, high-velocity powder and dry, flowing avalanches will not be substantially reduced in velocity by catching dams. This is confirmed by field observations of avalanches that indicate high-velocity avalanches may flow up and over terrain irregularities without depositing much of the mass and possibly without significant velocity reduction. Furthermore, it is possible that catching dams can serve as launching ramps for high-velocity avalanches which, having been launched, may descend upon objects from above. Thus, dams should not be built directly above buildings or other structures when high-velocity avalanches are expected.

RETARDING STRUCTURES

Purpose

The purpose of retarding structures is to shorten the runout distance of flowing avalanches by increasing ground friction and modifying the flow characteristics of the avalanches. This is accomplished by placing flow obstructions in the avalanche path that cause lateral spreading, decrease the mean flow depth, and increase frictional resistance within the flow.

Terrain Most Suitable for Retarding Structures

Retarding structures are most effective at locations where large avalanches begin to decelerate naturally, s with deflecting and catching structures. In general, hey are most effective on gradients of less than 20°, reas which often correspond to the runout zones of mall to medium sized avalanches. If high-velocity, drynow avalanches are the design case, catching strucures may not be effective on slopes steeper than 15°. Because of the high velocity and large flow depth of powder avalanches, their runout length will not be educed significantly by retarding structures.

Because retarding structures should be able to spread the flow laterally, unconfined areas of the runout zone will be more suitable for their placement than confined areas. In confined parts of the avalanche path, basal and turbulent frictional forces can be increased, but the average flow depth will not be reduced. Because of this, it can be stated that, in general, retarding structures will not be as effective on confined avalanche paths as the same structures would be on unconfined paths.

The possible effect of avalanches smaller than design size must be considered in design, placement, and maintenance of retarding structures. These avalanches will also be stopped by the retarding structures. The deposits from these smaller slides may reduce the effective height of the structures, reduce ground and structure frictional forces, and greatly reduce the effectiveness of the defense system against the larger avalanches. If deposition from smaller avalanches is thought to be a problem, it may be necessary to remove the debris after such avalanches. Removal should be done only when avalanche hazard is low.

Types of Retarding Structures

Two types of retarding structures have been used, earthen mounds and structural breakers (figs. 26, 27). Earthen mounds are effective if properly placed and are relatively inexpensive because they are composed of locally available, unconsolidated material that can be pushed into conical piles. Earthen mounds need not be designed for avalanche impact if the soil is the sandy-gravel-boulder type often found in avalanche paths. Disadvantages include the extensive earthwork and large base area required by the mounds which may result in extensive scarring of the terrain and the difficulty of removing snow from between the mounds.

Structural avalanche breakers can be used instead of mounds. However, these structures must be designed for avalanche impact and must be sufficiently large to affect the flow of the design avalanche. Because of design and construction costs, structural breakers tend to be more expensive than earthen mounds. An important advantage of structural breakers is that extensive earthwork is not required, allowing the natural ground surface to be retained between individual structures. Structures may be placed in such a way as to enable easy access for snow removal if this becomes necessary.

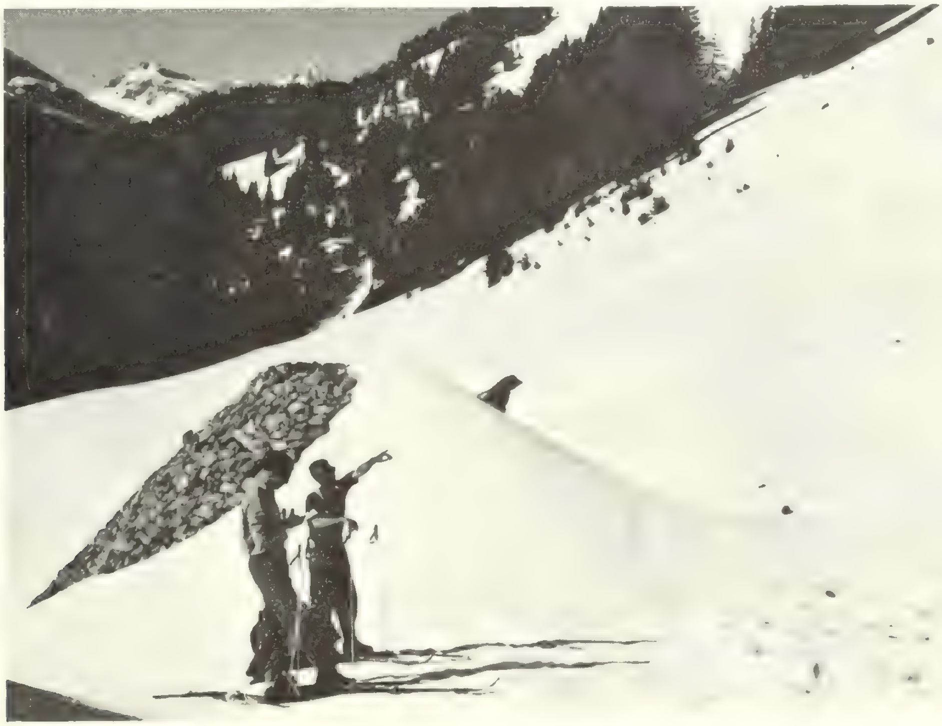


Figure 26.—Earthen mounds used as retarding structures. (Matt stock avalanche near Amden, Switzerland, USDA Forest Service photo)

Design of Retarding Structures

As with other types of structural defenses in the lower track and runout zone, design of retarding structures requires knowledge of the characteristics of the design avalanche. The required design parameters include velocity, flow height, and flow density. These parameters must be calculated, as discussed in section 2, prior to the design of structures.

The design height H of structures should be equal to or greater than the sum of the design snowpack height h_0 and the avalanche flow height h'. Thus,

$$H = h_0 + h' \qquad [32]$$

High-velocity avalanches tend to overtop the uphill structures (the first reached by the avalanche), but this is not a major problem, because the combined effects of increased boundary friction and forced lateral spreading will decrease avalanche velocity downstream.

The most effective array of structures is shown in figure 28. An array of this type will tend to spread the avalanche laterally, thereby decreasing the flow depth, and to increase mean boundary friction by effectively forcing the avalanche through a series of channels.

DIRECT-PROTECTION STRUCTURES

Purpose

Direct-protection structures can be used when individual, isolated objects must be protected from avalanche impact. In many cases in the United States and Europe, this type of defense has proven to be most practical because the necessary construction can often be incorporated into the design of buildings and can also take place on private property (figs. 29, 30, 31). Although direct protection may often appear to be the simplest and most economical means of avalanche protection, it is not appropriate in all situations. When several adjacent buildings need to be protected, diverting the flow by use of certain types of direct-protection structures may actually increase the avalanche hazard by changing the runout zone to a location not normally reached by the avalanche. Care must be taken in advanced planning to avoid such complications. In general, direct protection is probably not suitable for closely spaced buildings.

Terrain Where Direct Protection is Most Suitable

As with deflecting structures, direct-protection structures are most effective on slopes of 12-20°. On steeper slopes, avalanches will generally have high velocities, and on less steep slopes they may cause deposition against the object such that their effectiveness against future avalanches is reduced. Small slope gradients will not be a problem on the lower parts of long runout zones reached infrequently by avalanches. At these locations, the probability that a second avalanche will reach the protected structure while the debris from previous avalanches is still present can usually be disregarded.

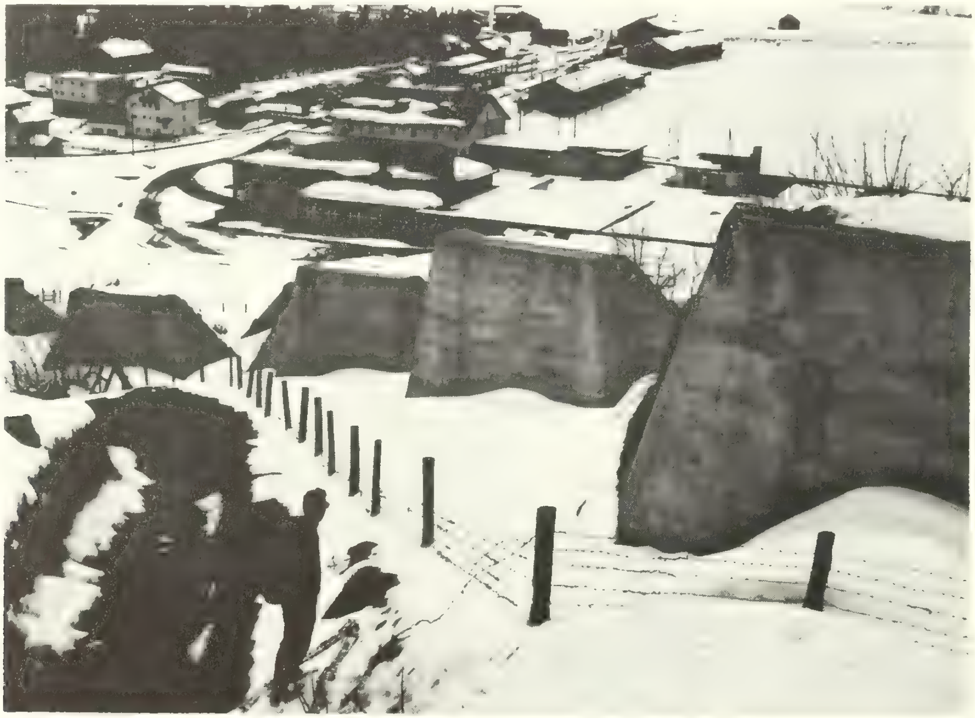


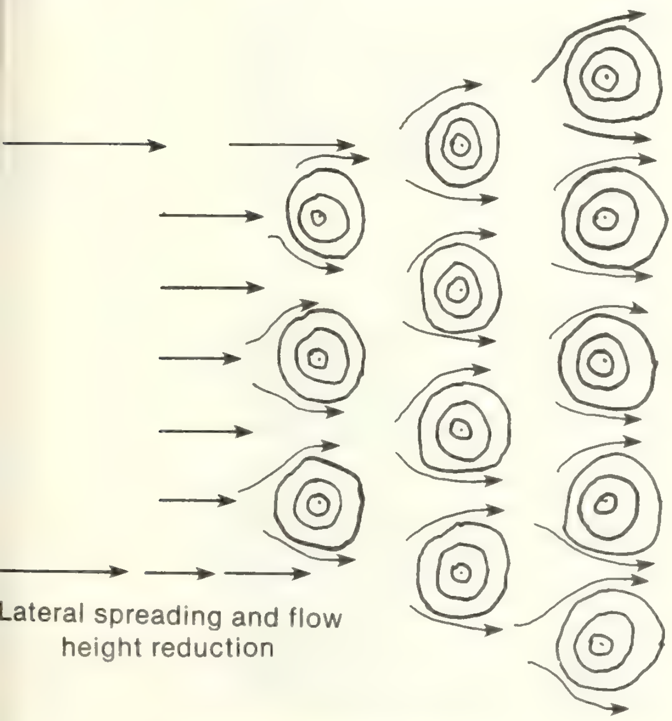
Figure 27.—Retarding structures above the army barracks near Andermatt Switzerland. (USDA Forest Service photo)

Necessity of Design Criteria

As with the other types of structures already scussed, the natural characteristics of the design alanche must be determined prior to design of the ructure. Essential information which should be deterined beforehand includes type or types of avalanches aching the defense site, avalanche velocity, flow epth, and density. This information enables design in rms of structure height and strength.

Cost of Direct-Protection Structures

Recent experience with direct-protection structures igs. 30, 31) at Vail, Colo., provides approximate stimates for architectural and engineering costs of uch structures. For example, the building shown in gure 30 has a reinforced back wall designed to withtand an impact pressure of 600 lb/ft² (2.9 t/m²). ngineering and architectural fees related to the esign of this wall were approximately $5,000-8,000 in 978. This cost was shared by two families. It is ineresting to note that in this particular case the addiional engineering costs were only 2-4% of the total onstruction cost and are a much smaller percentage f the present (1979) market value of this two-family welling (estimated to be more than $500,000). In this articular case, the construction costs of the wall are ifficult to estimate because such costs were combined vith other general costs. However, as a very rough stimate, additional construction costs of direct protecion did not exceed the engineering and architectural osts.



igure 28.—This array of earthen mounds reduces the runout distance by reducing the avalanche flow depth and increasing the frictional forces between the avalanche and ground.

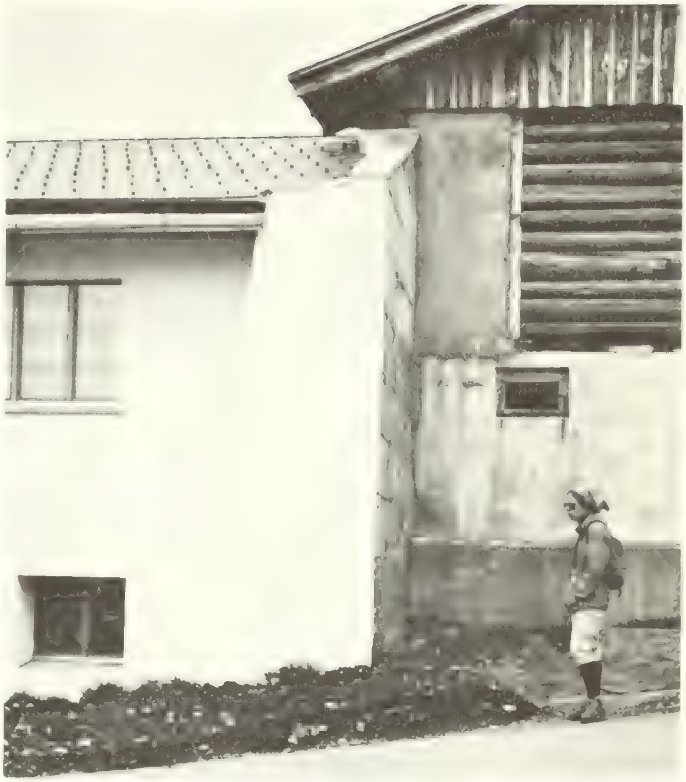


Figure 29.—This reinforced building wall near Davos, Switzerland, is designed to withstand avalanche impact. The wall surface is approximately normal to avalanche flow.

Design of Direct-Protection Structures

Direct-protection structures should be designed for fluid-dynamic stagnation pressures and for impact pressure from the dense, lower portion of flowing avalanches, or both. Calculation of these pressures should follow the steps outlined in the sections on Avalanche Impact and Deflecting and Guiding Structures.

In summary, the relevant equations to be used in direct-protection design are as follows:

1. The stagnation pressure when high-velocity, deep powder avalanches completely engulf an object. This is given by equation [12],

$$P_S = 1/2\rho' V^2$$

where ρ' is the bulk density of the flowing avalanche and V is avalanche velocity.

2. Impact pressure when the dense, lower portion of flowing avalanches hits a structure. This is given by equation [11],

$$P_f = K\rho' V^2$$

where $1.0 \leqslant K \leqslant 2.0$, depending on the compressibility of the design-avalanche snow upon impact.

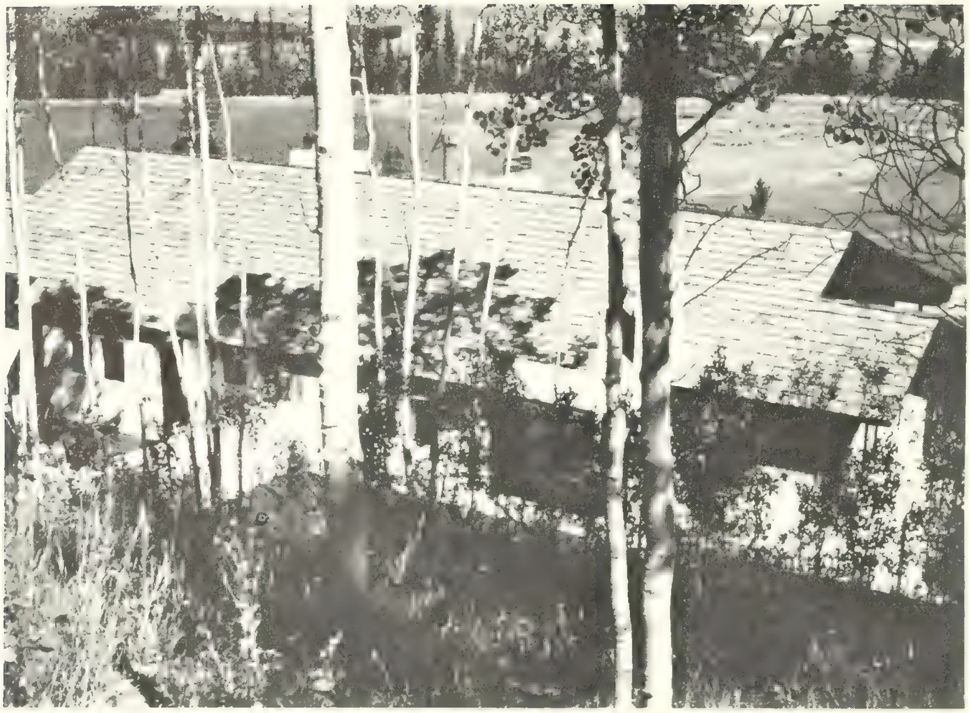


Figure 30.—This two-family dwelling is located below a small avalanche path at Vail, Colo. (fig. 1), and is designed to withstand an impact pressure of 600 lb/ft^2 (2.9 t/m^2).

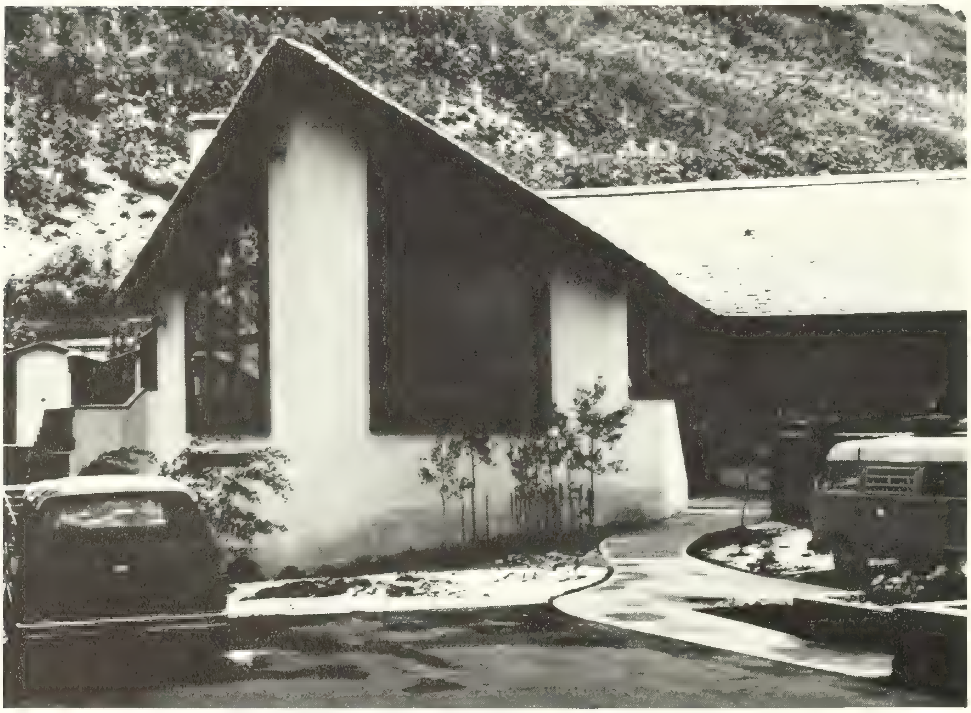


Figure 31.—This restaurant at Vail, Colo., lies within the runout zone of mixed motion and powder avalanches. The windows are artificial—the wall actually consists of reinforced concrete.

The total drag force F_d resulting from a powder valanche that engulfs the object is calculated from quation [13].

$$F_d = C_d A_d (\rho' V^2/2)$$

nd the lift force, F_l, on the same object is calculated rom equation [14].

$$F_l = C_1 A_1 (\rho' V^2/2)$$

where C_d and C_1 are drag and lift coefficients, respecively, and A_d and A_1 are areas exposed normal to and parallel to the avalanche flow, respectively. These equations are discussed more fully in the section on Avalanche Impact.

The design forces on a vertical surface exposed to avalanche impact must be determined in exactly the same way as previously described for vertical, straight, deflecting walls (section on Deflecting and Guiding Structures). Design height H is computed from equation [18],

$$H = h_0 + h' + (V \sin \phi)^2/2\ g$$

where h_0 is the snowpack depth, h' is the avalanche flow depth, V is the avalanche velocity, and ϕ is the deflection angle. Normal pressure P_n is computed from equation [19],

$$P_n = \rho' (V \sin \phi)^2$$

Shear in the avalanche direction P_x and vertical shear P_v are related to normal pressure P_n by the following expression:

$$0.5 P_n = P_x = P_v$$

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Guidelines are given for the design and location of deflecting, catching, retarding, and direct protection structures. Terrain, snow conditions and type, and frequency of avalanches are among the most important criteria for planning structural control of avalanches in the lower track and runout zone.

Keywords: Avalanche, avalanche dynamics, avalanche control, avalanche control structures, avalanche defenses.

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U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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Wetland Vegetation, Environmental Factors, and Their Interaction in Strip Mine Ponds, Stockdams, and Natural Wetlands

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Abstract

Water regime, chemical features, temperature factors, light penetration, substrate properties, and physical characteristics are described for Northern Great Plains strip mine ponds and stockdams, followed by a discussion of how their interaction determines wetland plant community composition and resulting wildlife habitat quality for consumptive and nonconsumptive resource utilization.

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Wetland Vegetation, Environmental Factors, and Their Interaction in Strip Mine Ponds, Stockdams, and Natural Wetlands[1]

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Richard A. Olson

Management Implications

Thousands of impoundments in the form of coal strip mine ponds, stockdams (stockponds formed by damming natural drainages), and dugouts (stockponds formed by excavating large pits) have been constructed where natural wetlands are largely absent in the unglaciated areas of the Northern Great Plains. These specialized ecosystems can be managed to provide natural resource consumers with values similar to those provided by natural wetlands of the prairie pothole region. However, land management plans are needed if these constructed impoundments are to improve wildlife habitat, fishery habitat, irrigation, water sources for livestock, and recreational activities.

The associated wetland plant communities on these constructed impoundments should be a major concern in developing management plans since this ecosystem component supports a variety of wildlife species through the habitat it provides, particularly for waterfowl. Escape cover, nesting cover, brood rearing cover, and food sources (both vegetative and faunistic), all required by waterfowl, are found in wetland plant communities. In addition, recreational activities such as bird-watching, wildlife photography, hunting, trapping, fishing, and aesthetic endeavors are enhanced by the presence of diversified, well-developed wetland plant communities.

Existing strip mine ponds on the Northern Great Plains commonly are characterized by precipitous shorelines, few shallow areas, steep spoil piles, and heavy erosion. Most of these impoundments, especially the most recently mined, exhibit sparse growth of wetland vegetation and contribute little to the availability of wildlife habitat. On the other hand, stockdams with gently sloping shorelines, many shallow areas, and little erosion generally display lush, well-developed wetland vegetation zones except where heavy livestock use prevails. Heavy livestock use around stockdams tends to disrupt wetland vegetation and reduce the quality of wildlife habitat through grazing activity, trampling, and increasing erosion and sediment loads into the wetland basin. Management plans for these constructed impoundments could alleviate major problems and enhance wetland vegetation for both consumptive and non-consumptive resource utilization.

The development of wetland vegetation in Northern Great Plains impoundments is governed by a host of complex, interacting environmental variables such as water regime, water chemical features, water temperature factors, light penetration, submerged substrate properties, and basin physical characteristics. The nature and presence of specific plant species reflect current environmental conditions of the aquatic ecosystem, resulting from the interaction of previously described environmental variables.

Before resource managers can develop management plans that will maximize multiple uses on these constructed impoundments, ecological relationships between biological, chemical, and physical factors must be well understood. A logical approach toward developing management plans is to determine the major environmental factors operating on wetland plant community expression, try manipulating these factors using a variety of techniques learned from future research, and incorporate those techniques which best produce the desired expression of wetland vegetation into the final management plan.

Herein lies the challenge for resource managers. We must first pool all the available information on the ecology of constructed impoundments, and then concentrate future research efforts on identifying influential environmental factors and the responses from manipulation techniques that optimize wildlife habitat value.

Our knowledge about the ecology of aquatic ecosystems on constructed impoundments is extremely limited as evidenced by a lack of publications dealing with ecological relationships on livestock ponds and only sparse information about wetland vegetation on strip mine ponds. Most of the information available for strip mine ponds deals with reclamation of terrestrial vegetation.

The implications of developing management plans for these constructed impoundments are far reaching, especially in light of rapid, future development of energy sources. As energy development continues, more habitat for wildlife will be disrupted or destroyed, more public land for consumptive and nonconsumptive resource uses will be closed or reduced in area, and new, potentially valuable wetland basins will emerge. Resource managers must be prepared to intensively manage these new habitat parcels to optimize multiple use value and restore habitat value in previously disturbed impoundments.

Introduction

Constructed impoundments are becoming more numerous in the Northern Great Plains each year. Coal strip mine ponds—formed when surface mine pits fill with underground water, precipitation, and runoff—are becoming more prevalent in North Dakota, South Dakota, Wyoming, and Montana as the demand for energy increases. During 1966, approximately 53.8 quadrillion Btu's of energy were consumed in the United States. By the year 2000, an estimated 159 quadrillion Btu's will be required annually. Demand for coal as an energy source is estimated to be 53% greater in 1980 compared with 1967, and will be 78% greater in the year 2000 compared with 1980 (Bureau of Mines 1971).

Lignite coal, the predominate type in North and South Dakota and sub-bituminous coal, the predominate type in Wyoming and Montana, are used mainly for generating electric power. Large reserves of these coals in the Northern Great Plains make strip mining methods profitable. Averitt (1973) estimated total coal reserves (with an overburden of 0-915 m) of North Dakota at 317.9 billion metric tons (all lignite); South Dakota, 1.8 billion metric tons (all lignite); Wyoming, 109.4 billion metric tons (11.5 bituminous, 97.9 sub-bituminous); and Montana, 201.1 billion metric tons (2.1 bituminous, 119.5 sub-bituminous, and 79.5 lignite). These totals represent 57% and 98% of all sub-bituminous and lignite reserves in the United States respectively. As of January 1, 1976, total lignite mined in North Dakota by stripping methods was 156.9 million metric tons or 1% of the total strippable resource (Bluemle 1977). As more rangeland water impoundments emerge from intensified future strip mining activity, the demand for more intensive management plans on these ecosystems will increase.

Other types of constructed water impoundments becoming increasingly numerous are stockdams and dugouts. Approximately 220,000 stockdams and 40,000 dugouts were constructed in North Dakota, South Dakota, eastern Wyoming, and eastern Montana by 1964 (Bue et al. 1964) . These figures represent estimates from U.S. Department of Agriculture records for impoundments constructed with federal assistance and by private landowners. Since 1964, the number of these impoundments on the Northern Great Plains has probably doubled. Although the exact number of stockdams and dugouts is not known, they contribute to the diversity of rangeland ecosystems.

Associated wetland plant communities, common to all three constructed impoundments, are one of the more important components of these ecosystems. These plant communities provide habitat to a variety of fauna for both consumptive and non-consumptive resource use.

Most research involving wetland plant communities has focused primarily on natural wetlands of the prairie pothole region. Little research has been conducted on wetland vegetation of coal strip mine ponds, stockdams, and dugouts. A large amount of information is available concerning reclamation of strip mines i the eastern United States. However, most of this info mation focuses on reclamation of terrestrial vegetatio on strip mine spoil banks with little or no emphasis o the wetland vegetation in strip mine ponds. Wetlan vegetation analyses of strip mine ponds, stockdams and dugouts in the Northern Great Plains are nc available. There is a great need for research on th taxonomy, ecology, and biology of wetland plant com munities associated with these constructed water im poundments (Kadlec and Wentz 1974).

Objectives

The purpose of this paper is to consolidate curren information on the ecology of wetland vegetation an associated environmental factors from strip min ponds, stockdams, and dugouts with supplemental in formation on natural wetlands. This reference is a preliminary source to assist researchers, educators and resource managers prior to full-scale investigations of wetland vegetation on Northern Great Plains strip mine ponds, stockdams, or dugouts.

This paper describes (1) the need to develop more intensified management plans for strip mine ponds, stockdams, and dugouts, especially in light of increased future strip mining activity, (2) the formation and physical characteristics of these diversified rangeland ecosystems, (3) the history of wetland vegetation studies, (4) major environmental factors functioning on constructed impoundments, and (5) the interaction between environmental factors and wetland plant communities.

Physical Characteristics of Constructed Impoundments

Strip mine ponds originate from open-pit mining where soil overburden is removed by power shovels, draglines, and tractor-drawn scoops to reach coal seams situated at shallow depths below the soil surface. In earlier mining processes, overburden was deposited in long ridges (ridge height varying with overburden thickness) parallel to the exposed cut as coal removal continued at right angles to the spoil piles. Long, narrow valleys 3-8 m deep were formed between ridges of spoil material. The final cut, with overburden and coal removed, often filled with water, forming a lake or pond surrounded by steep, high banks (fig. 1) (Crawford 1942, Riley 1954, Brewer and Triner 1956). Overburden removal buried nontoxic surface materials underneath the spoil pile and exposed toxic acid material from soil layers directly above the coal seam. Oxidation of these toxic materials and subsequent runoff from spoil piles resulted in sulfuric acid accumulation in the impoundment, causing the problems associated with older strip mining methods (fig. 2) (Riley 1960).

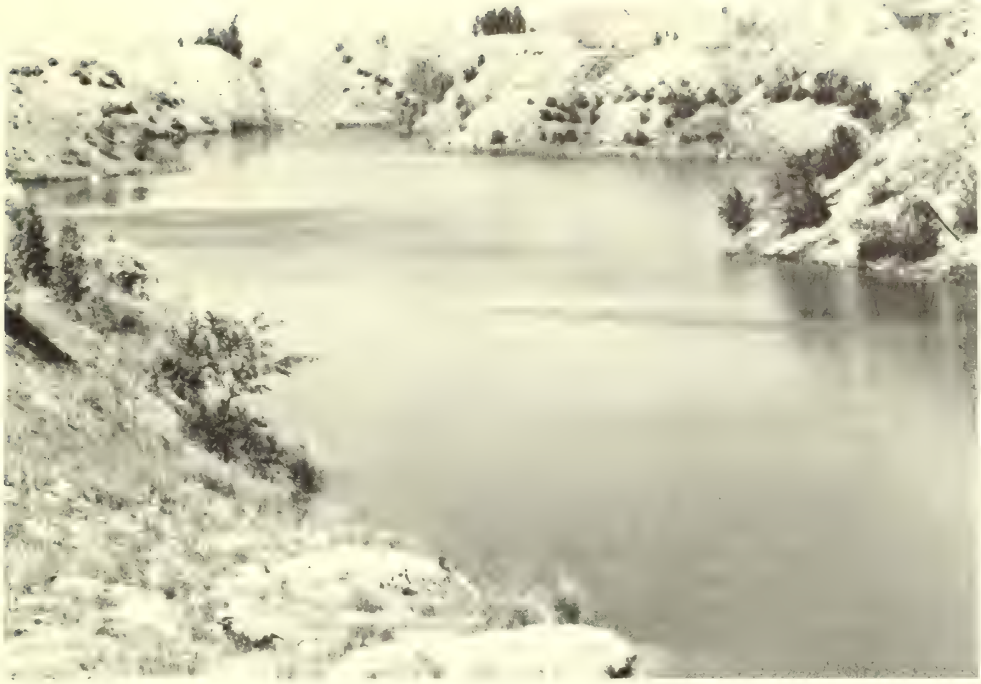

Figure 1.—Precipitous shorelines, few shallow areas, restricted water-level fluctuations, and steep spoil piles with extensive bare exposures, a result of early strip mining activity, are major factors limiting development of wetland vegetation on these constructed impoundments. Water from underground aquifers filled the abandoned open-pit mine forming a strip mine pond.

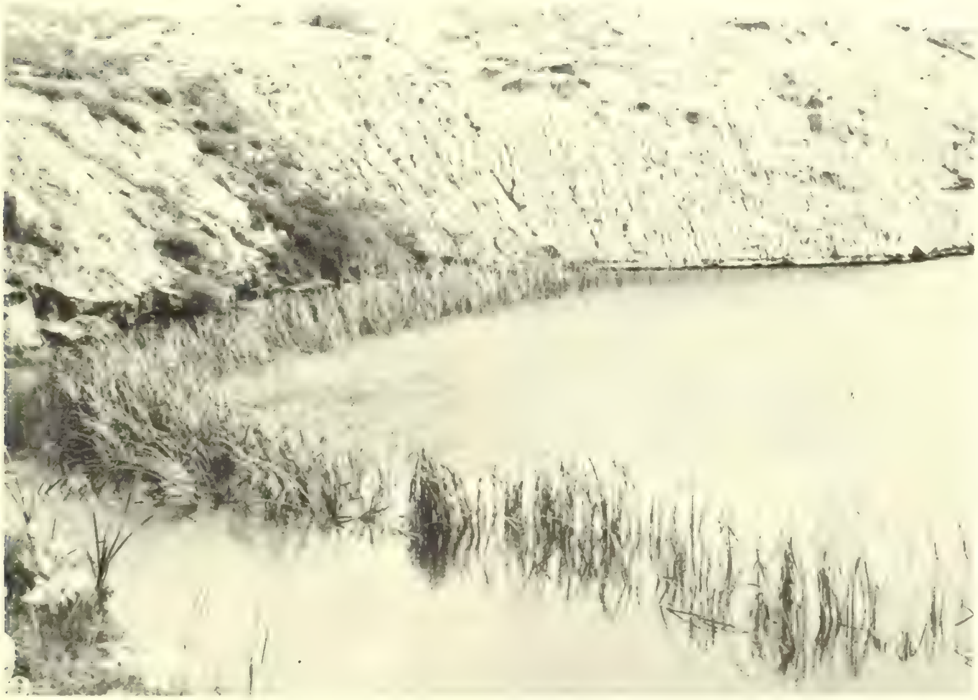

Figure 2.—Oxidation of toxic sub-surface spoil material from surrounding spoil banks, combined with subsequent runoff and erosion, directly determine the chemical composition of basin water. Acting as storage reservoirs for toxic pollutants carried in runoff, the aquatic habitat of these impoundments often retard wetland plant development.

The increased strip mining activity in recent years on the Northern Great Plains, has prompted more stringent federal laws controlling surface mining reclamation. Within these federal guidelines, individual states have adopted their own regulations regarding surface mining reclamation. In many cases state laws are more stringent than the guidelines established by the federal government.

In North Dakota, surface coal mining operators are required to match the surrounding topography in reclamation efforts and "restore the land affected to a condition capable of supporting the uses which it was capable of supporting prior to any mining." The creation of any permanent water impoundment must be approved by state regulatory agencies through detailed mining and reclamation plans before mining permits are issued. Planned water impoundments must meet specific standards determined by state engineers.[2]

In Wyoming, the final exposed mining pit and surrounding spoil material must be "sloped, graded, and contoured so as to blend in with the topography of the surrounding terrain and provide for access and revegetation." Steep, parallel ridges of spoil material are not allowed under today's stricter reclamation laws (Department of Environmental Quality 1978). Montana and South Dakota have similarly strict reclamation laws governing the final appearance of strip mined areas.

Most older strip mine ponds are characterized by precipitous shorelines, absence of shallow areas, and presence of steep spoil piles with extensive bare exposures limiting the production of vegetation and fish. Such ponds vary from less than 1 ha to several hectares in surface area with a long, narrow configuration to the basin (Lewis and Peters 1955, Davis 1971, Coe and Schmelz 1972).

Bell (1956) found that in southern Illinois, intensive erosion of the 40-60° soil slopes produced a narrow, mucky shelf around the pond perimeter. Burner and Leist (1953) reported that in Kansas, older spoil piles have rounded ridges caused by erosion and crumbling of spoil material.

Working in Missouri, Parsons (1964) classified strip mine ponds into two types based on continuity of the water mass and shoreline length. One type, called "chevron" ponds, were characterized by having 90-95% uninterrupted water areas (linkages between ponds flooded) with extensive shoreline length, compared to surface area. A second type, called "parallel" ponds, had 50% or less uninterrupted water area (linkages between ponds interrupted with land mass) with restricted shoreline length, compared to surface area. Riley (1960) found strip mine ponds in Ohio with water depths less than 7.5 m, and with underground springs and runoff as the principle water supplies.

Stockdams in the Northern Great Plains are formed by constructing dams (earthen or concrete) across natural drainage routes, forcing water to accumulate and form an impoundment. Dugouts, in contrast to stockdams, are large excavated holes designed to catch runoff or intercept ground water. Spoil from dugouts is placed parallel along the sides of the excavated hole. Both stockdams and dugouts are constructed primarily to provide water for livestock although other benefits such as wildlife habitat accrue (Bue et al. 1964).

Stockdams on the Northern Great Plains are wetland basins having gently sloping shorelines except at the dam, having surface areas from less than 1 to 16 ha containing maximum depths of less than 1-6 m, and with runoff as the principal water source (fig. 3) (Bue et al. 1964). Bue et al. (1964) noted that aquatic vegetation will appear during the second year on a newly constructed pond and become established in 3-5 years.

Strip mine ponds, stockdams, and artificial wetlands can be considered "wetlands" according to a broad definition which refers to any lowland area containing water, and ranging from basins or flats which undergo seasonal submergence to lands which are waterlogged or flooded at all times (Martin et al. 1953, Shaw and Fredine 1956, Cowardin et al. 1979). The term wetlands encompasses marshes, swamps, potholes sloughs, ponds, and shallow lakes.

Some strip mine ponds and stockdams probably possess a potentially longer lifetime than that of natural wetlands, because the artificial ponds have greater water depths, a more permanent water table, and larger watershed areas (Golet and Larson 1974). Dineen (1953), in a study of a Minnesota pond, found that annual deposition of organic matter from emergent plants was a major factor in reducing the area and depth of small ponds.

History of Wetland Vegetation Studies

Early studies of aquatic macrophytes, largely conducted in north-central United States, were primarily descriptive, with their authors emphasizing the floristic composition (Stout 1913, Pearsall 1920, Denniston 1921, Rickett 1921, 1924, Butcher 1933, Thomson 1944, Love and Love 1954). These studies usually included some environmental effects on wetland vegetation and were forerunners of more ecologically-oriented floristic investigations such as Graham and Henry (1933), Wilson (1937), Misra (1938), Potzger and Van Engel (1942), Swindale and Curtis (1957), Mandossian and McIntosh (1960), Modlin (1970), and Zutshi (1975).

Wetland plant studies evolved into complex investigations directed at the "ecosystem." More recent ecological investigations of wetland vegetation attempt to define environmental-edaphic-vegetation relationships using a variety of statistical analyses, including simple correlation techniques, gradient analysis, and principal components analysis (Walker and Coupland 1968, Van der Valk and Bliss 1971, Walker and Wehrhahn 1971, Dirschl and Coupland 1972, Auclair et al. 1973, 1976a, 1976b and Kologiski 1977).

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[2] *North Dakota Surface Mine Reclamation Act. 1979. Environmental protection performance standards, chapter 38-14.1-14.7, North Dakota Century Code, Bismarck, N. D. Draft proposal.*

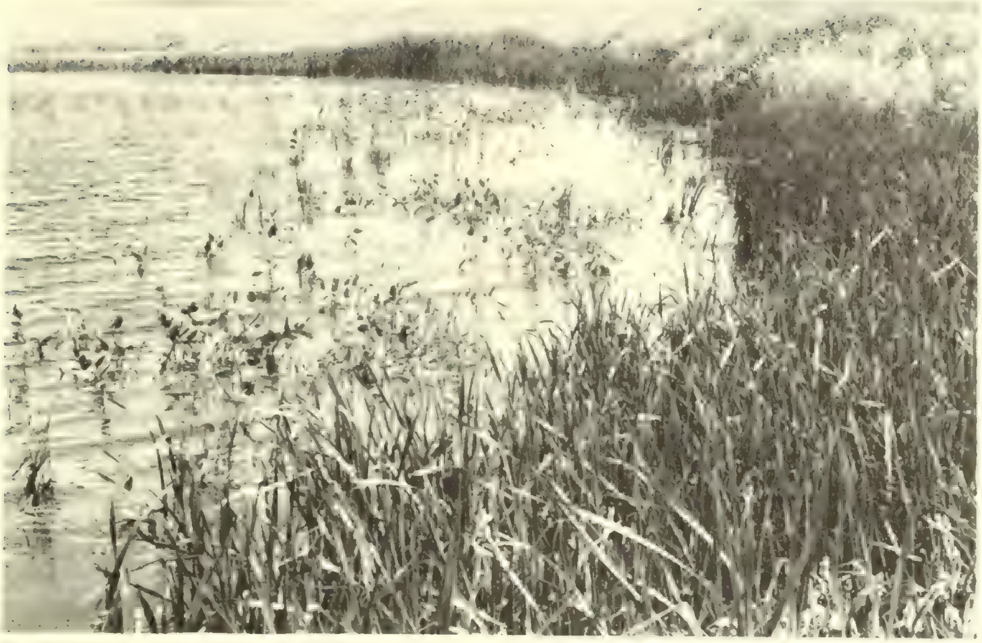

Figure 3.—Stockdams, formed by constructing dams across natural drainage routes, support more extensive wetland vegetation development due to gently sloping shorelines and absence of disturbed surface soil material.

Information available on strip mine ponds and associated wetland vegetation frequently is part of a more inclusive limnological investigation (Burner and Leist 1953, Lewis and Peters 1955, Simpson 1961, Parsons 1964, Tobaben 1969, Campbell and Lind 1969, Davis 1971, Coe and Schmelz 1972). However, Bell (1956) in Illinois, Dinsmore (1958) in Pennsylvania, and Riley (1960) in Ohio focused primarily on the ecology of wetland vegetation in strip mine waters. Less information is available on the ecology of wetland vegetation in stockdams and artificially created wetlands than on strip mine ponds. Dane (1959) and Lathwell et al. (1969) have conducted ecological investigations on artificially created marshes in New York.

There is considerably more literature addressing the ecology of wetland vegetation on natural wetlands of the prairie pothole region. Occasionally this literature is cited in this report to supplement the lack of available information on strip mine ponds and stockdams in order to provide the reader with an example of ecological relationships on constructed impoundments.

Environmental Factors Functioning on Constructed Impoundments

Ecological studies of wetland vegetation cannot be restricted to vegetational aspects alone, but must include various environmental factors which interact to produce the expression of wetland plant community structure. An understanding of how environmental factors function, their interaction, and their relationship to wetland vegetation is necessary before management plans can be formulated.

Water Regime

Seasonal water levels fluctuates to some degree in all wetland basins through inflow and outflow pathways. These fluctuations can be beneficial to wetland plant establishment, provided the magnitude of fluctuation is not excessive. Moderate fluctuation provide optimum moisture conditions suitable to a wider diversity of wetland vegetation. Studying Illinois strip mine ponds, Bell (1956) found extreme fluctuations in water level caused by unmoderated overflow from steep basin slopes, lateral movement of subsurface water away from the pond through surrounding porous spoil materials, and restricted size of the watershed. Rapidly changing water levels on steep sloped strip mine ponds produce quick, extreme changes in moisture conditions to which many wetland plants are unable to adapt. As a result, plant species composition and density is limited.

No information is available on the magnitude of water level fluctuations in stockdams and its effects on wetland vegetation establishment. More research is needed in this area before development of management plans for these ecosystems.

However, considerable work on the hydrology of natural wetlands indicates that the water budget on these ecosystems involves gains from inflow and losses from outflow (Eisenlohr 1965, 1966, 1967, 1969a, 1969b, 1969c, 1972, Eisenlohr and Sloan 1968, Shjeflo 1968, Sloan 1970, 1972). The magnitude of water level fluctuations from inflow and outflow water budgets on natural wetlands, in terms of water depth in wetland plant communities, is minimized by characteristic shallow basins. As a result, a greater variety of wetland plant species can tolerate the more favorable moisture regime.

Major sources of water inflow into wetland basins are through direct precipitation, surface runoff from the surrounding watershed, and seepage inflow from ground water tables. The amount of water entering a wetland in spring is determined by the amount of snow accumulation in the watershed, intensity of snowmelt caused by prevailing air temperatures, level of soil moisture at freeze-up, and depth of frost penetration in the soil during the preceeding fall (Millar 1969b, Daborn 1976).

Water outflow is primarily by evaporation from the water surface, evapotranspiration from marginal vegetation, seepage outflow from the pond bottom, and overflow around pond margins.

Presence of extensive marginal emergent vegetation complicates the water regime of a wetland by both (1) reducing water loss from evaporation by sheltering the water surface from wind and radiation and (2) increasing water loss through evapotranspiration (Eisenlohr 1965, 1969a). Eisenlohr (1965) found that plant evapotranspiration rates at the beginning and end of a growing season were less than evaporative loss from the free water surface. However, total evapotranspiration loss for the entire growing season on a prairie pothole filled with vegetation may be greater than the evaporation rate if no vegetation were present.

In dry years when evapotranspiration is higher, water loss from a wetland filled with vegetation may be excessive enough to deplete moisture conditions required by wet meadow plant communities located on the outer fringes of the wetland basin. In this situation, wetland plant composition may change resulting in decreased waterfowl nesting and feeding areas. To minimize water loss from a wetland basin through evaportation or evapotranspiration, wetlands completely filled with vegetation should be opened by blasting or other mechanical means to decrease water lost through evapotranspiration. On sparsely vegetated wetlands, management practices such as contouring basin slopes and water level control should be considered as a means to encourage wetland plant development along basin margins to decrease water loss by evaporation. Again, more research is needed on water loss in constructed impoundments so management plans can be developed from sound field information.

Likewise, removal of peripheral vegetation through cultivation or grazing may reduce spring runoff into the wetland by reducing the amount of accumulated snow "trapped" by vegetation and/or reduce water loss from the basin by removal of potentially transpiring plants (Millar 1969a). However, removal of peripheral vegetation may also increase water loss by evaporation. Ideally, a certain amount of marginal wetland vegetation is needed to prevent evaporation loss and maintain optimum moisture conditions for wetland vegetation. Future research is needed to determine the specific degree of vegetative development required to optimize moisture conditions for wetland plant communities.

Working with small wetlands, Millar (1971) found that the rate of water loss per unit area varied directly with the length of shoreline and inversely with the size of individual wetlands. Water loss was principally by lateral seepage to transpiring marginal vegetation, evaporation from shoreline soil surfaces, and seepage to groundwater. He stated that during the growing season 60-80% of the shoreline water loss could be attributed to transpiration by marginal phreatophytic vegetation and evaporation from the soil surface. Shoreline-related water loss accounted for 60% or more of total water loss in wetlands .04 ha or less in size and 30-35% in wetlands greater than 1 ha.

Fluctuating water regimes also influence the concentration of dissolved solids in a wetland and may effect wetland plant community composition in some situations. Evaporation from the water surface, evapotranspiration from marginal vegetation, runoff entering a wetland, and seepage inflow all tend to increase the concentration of dissolved solids while direct precipitation on the wetland, seepage outflow, and overflow reduce the concentration of dissolved solids (Eisenlohr 1969a, Rozkowska and Rozkowski 1969, Sloan 1970). Eisenlohr (1969a) found wetlands fresher at higher elevations due predominately to the flushing effect from seepage outflow, compared to wetlands at lower elevations where dissolved solids concentrated under predominate seepage inflow effects.

An excessive amount of dissolved solids may create highly turbid water which could limit light penetration to photosynthesizing submerged vegetation thus restricting submerged plant development at certain water depths. Also, high concentrations of dissolved solids may become toxic to wetland vegetation.

A common cause of turbidity in stockponds is excessive livestock grazing which promotes greater silt loads entering the wetland basin from runoff erosion. Management practices which restrict grazing around wetland basins, encourage greater vegetative development around the pond periphery, and minimize water loss by evaporation and evapotranspiration should result in minimum dissolved solid concentrations.

Water Chemistry

Although the chemical composition of water varies from wetland to wetland, certain features are common to older strip mine ponds and artificial wetlands in the Northern Great Plains. Strip mine ponds possess unique water chemistry, a factor that could explain, in part, differences in wetland plant composition in comparison to natural wetlands.

The chemical condition of water in strip mine ponds is a direct result of runoff from exposed materials in the surrounding spoil banks. These wetland basins act as storage or holding reservoirs for toxic pollutants carried in runoff (Crawford 1942, Riley 1954, 1960, Lewis and Peters 1955, Dinsmore 1958, Parsons 1964, Struthers 1964, Campbell and Lind 1969, Davis 1971, Coe and Schmelz 1972). A build-up of toxic pollutants in these wetland basins can limit certain nontolerant wetland plant species and decrease the diversity and value of wildlife habitat. As toxicity increases, usually on newer strip mine ponds, other normally tolerant plant species will disappear.

During the older stripping process, overburden was removed to expose the underlying coal seam. Subsoil originally on top of the coal seam was deposited on top of the spoil pile, exposed to air and precipitation. Oxidative processes after materials are exposed to air and water, convert raw materials into acids and salts which accumulate in the basin. Studying older strip mine ponds, Crawford (1942) in central Missouri, Dinsmore (1958) in Pennsylvania, Riley (1960) in Ohio, Simpson (1961) in Kansas, Struthers (1964) in Ohio, and Davis (1971) in western Maryland all reported toxic conditions for flora and fauna caused by the decomposition of marcasites, pyrites, and black amorphous pyrites (all forms of iron sulphides) into sulfates and sulfuric acid residues.

In the Northern Great Plains, acidic conditions do not appear to be a major by-product of oxidative reactions on spoil material. Most of the reported residues from oxidative processes are sulfate salts, which can also be toxic to wetland vegetation under high concentration. Sandoval et al. (1973), working with spoil bank material from various North Dakota sites, found sodium sulfate salts to be the major constituent leached from spoil material. Hinkley and Taylor (1977) and Ringen et al. (1979), working near Sheridan, Wyo., found magnesium sulfate salts to predominate in both spoil bank material and pond water. High salinity levels, as measured by specific conductance, can limit the number of plant species present. Stewart and Kantrud (1972) described a specific association of plant species for differing degrees of specific conductance. At extreme salinity levels even the most tolerant species cannot survive.

Hawkes and Anderson[3] found general alkaline conditions along with predominate sodium and magnesium sulfates in strip mine pond water throughout North Dakota, South Dakota, and Wyoming. For most wetland plant species, alkaline conditions are more favorable than acidic conditions.

Under current strict reclamation laws, strip mining operators on the Northern Great Plains must separate topsoil from subsoil, replacing each soil layer in proper perspective during reclamation activities so that revegetation can be successful. In North Dakota, state law requires mine operators to redistribute topsoil in a uniform manner after backfilling, compacting (to prevent soil erosion and leaching of toxic materials), and grading toxic subsoil.[2]

In Wyoming, topsoil and subsoil must also be segregated prior to mining and then replaced in the original sequence after mining. In addition, sources of possible water contamination within an impoundment area after reclamation must be "stablized in such a manner to prevent contamination of the impounded water" (Department of Environmental Quality 1978). Again, Montana and South Dakota have similar laws requiring separation of topsoil and subsoil prior to mining. These laws are geared towards providing environmental conditions suitable for vegetation re-establishment.

In ponds outside the Northern Great Plains, the degree of acidity present in a strip mine impoundment seems to be related to the age of the impoundment. Crawford (1942) in central Missouri, Parsons (1964) in eastern Missouri, Campbell and Lind (1969) in Missouri, and Coe and Schmelz (1972) in Spencer County, Indiana, all report considerably more acidity in younger strip mine ponds and consequently sparser wetland vegetation compared to older basins. Campbell and Lind (1969) described changes in acidity on Missouri ponds as a successional trend characterized by decreasing acidity (as indicated by increasing pH values) and increasing biological productivity, both for flora and fauna, with increasing basin age. They believe that weathering spoil piles release reduced quantities of sulfuric acid and total dissolved solids into the basin, allowing an increase in bicarbonate alkalinity concentration (which acts as a buffer in acidic conditions) and thereby creating alkaline conditions in aging ponds.

Increasing alkalinity creates more favorable conditions for the establishment of wetland plants ordinarily intolerant to acidic conditions. As alkalinity conditions increase, a greater diversity of wetland vegetation appears, to a point, improving wildlife habitat quality.

Generally, resource managers can do little to alleviate acidic conditions in new strip mine ponds without large expense and time involved. Also, any treatments would have to be a continued process over a long period until the leachate was nontoxic.

Crawford (1942) suggests neutralizing acidic conditions in central Missouri strip mine ponds by adding powdered limestone, marl, soda ash, caustic soda, or potash. However, such a process is expensive, time consuming, and requires a disposal area for the precipitated calcium sulfate sludge, which can be 20-40% of the treated water volume. Also, any new precipitation would leach additional salts and acids into the basin from surrounding spoils and destroy previous treatments.

More detailed information on specific chemical parameters effecting wetland vegetation was described by several investigators working on strip mine ponds outside the Northern Great Plains. Crawford (1942) in central Missouri, Burner and Leist (1953) in Kansas, Riley (1954) in Ohio, Lewis and Peters (1955) in southern Illinois, Bell (1956) in southern Illinois, Davis (1971) in western Maryland, and Coe and Schmelz (1972) in Indiana found water pH to be in the range from high acidity (pH 3.0), especially on younger ponds, to slightly basic (pH 8.2). In moderate acidic conditions only *Typha* species prevail, but as acidity decreases and alkalinity increases a wider variety of plant species can prosper. Under highly acidic conditions, pH of 4.0 and below, no species can survive. Generally, water pH of 7.0 and greater are required for adequate wetland vegetation establishment (Crawford 1942, Coe and Schmelz 1972).

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[3] *Hawkes, C. L., and M. T. Anderson. Physical and chemical features of strip mine ponds in the Northern Great Plains. I. Coal strip mine ponds. (Unpublished report at Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

Hawkes and Anderson,[3] working on strip mine ponds in North Dakota, South Dakota, and Wyoming from 1976 to 1978, found pH values ranging from 7.7 to 9.9. Generally higher alkaline conditions in ponds on the Northern Great Plains were not considered to be problematic for wetland vegetation on those ecosystems.

Burner and Leist (1953) in Kansas, and Davis (1971) in western Maryland, found identical pH values at the surface and bottom in their study ponds. In a southern Illinois study, Bell (1956) reported a noticeable decrease in the density of wetland vegetation at pH 6.6 with only emergent plant species present at pH values lower than 6.4.

Lewis and Peters (1955) in southern Illinois, Davis (1971) in western Maryland, and Coe and Schmelz (1972) in Indiana all reported high specific conductance values caused by high concentrations of dissolved salts. Specific plant species have been known to be associated with varying degrees of specific conductance of surface water (Stewart and Kantrud 1972).

Lewis and Peters (1955) found considerably lower specific conductance in surrounding farm ponds as compared with coal strip mine ponds. Davis (1971) reported slightly higher specific conductance at the bottom of Maryland strip mine ponds in comparison to surface readings. Values were highest during July, August, and September, the peak maturation period for wetland vegetation.

Hawkes and Anderson,[3] on the Northern Great Plains, found low salinity (as measured by total filterable residue) levels in coal strip mine ponds. Specific conductance on these impoundments during 1976-78 ranged from 500 to 5959 μmhos/cm. Hammer (1978), working on 60 lakes in the prairies of southern Saskatchewan, reported a range of specific conductance of 3,000-28,000 μmhos/cm.

Sulfate was the predominate anion in Kansas, Ohio, and Missouri strip mine ponds from the oxidation of toxic spoil materials and subsequent runoff (Simpson 1961, Struthers 1964, and Campbell and Lind 1969). Hawkes and Anderson[3] found similarly high levels of sulfate in 20 Northern Great Plains coal strip mine ponds with a range of 292-4894 mg/1. Rockett (1976) and Wangness (1977), both studying coal strip mine ponds near Sheridan, Wyo., also reported sulfate as the predominate anion in that region. Hammer (1978) reported sulfate as being the major anion in 53 of 60 prairie lakes he studied in southern Saskatchewan. In western Maryland, Davis (1971) found no significant difference in sulfate concentration between surface and bottom areas of his study ponds. Sulfate concentrations, in the form of sulfate salts, can be especially inhibitory to wetland vegetation at high concentration levels.

Crawford (1942) and Hawkes and Anderson[3] were the only investigators to report detailed information on the concentration of other mineral substances such as sodium, potassium, iron, manganese, calcium, chloride, and magnesium. However, Simpson (1961) and Campbell and Lind (1969) reported that calcium, magnesium, and iron were the dominate cations in Kansas and Missouri strip mine ponds.

Crawford (1942), working on Missouri strip mine ponds, stated that the concentration of all mineral substances followed seasonal changes. Of all minerals, calcium displayed the highest concentration in extremely polluted and acidic ponds. Magnesium concentrations were irregularly distributed in five Missouri ponds studied by Crawford (1942). Sodium occurred in smaller concentrations than either calcium or magnesium in all five study ponds. Potassium and iron concentrations were highest in the most acidic ponds. Finally, manganese concentrations were inversely correlated with hydrogen ion levels.

At excessive concentrations, any one of the mineral substances can become toxic to wetland flora. At this point, not enough information is known about manipulating environmental factors to control concentrations of mineral substances that may be toxic to wetland vegetation. Again, more research is needed on constructed impoundments to answer these questions.

Hawkes and Anderson[3] reported that the major cations on 20 coal strip mine ponds they studied on the Northern Great Plains were sodium and magnesium with concentration ranges of 5-365 and 32-1339 mg/l, respectively. Other concentrations of cations and anions that they reported were calcium 14-314 mg/l, potassium 11-48 mg/l, and chloride 3-49 mg/l. They commented that the major cations and anions present in their study ponds were directly related to the chemical composition of the surrounding mine spoil material. The expression of wetland vegetation development is likewise related to the chemical composition of pond water.

Among the organic macronutrients measured by Hawkes and Anderson,[3] total Kjeldahl nitrogen was highest in concentration with a range of 0.15-1.94 mg/l for all 20 ponds investigated. Total phosphorus and nitrate were represented by concentration ranges of 0-0.53 and 0-0.86 mg/l, respectively. These organic nutrients are probably the most important for plant growth and development. Drawdowns enhance presence of these macronutrients by allowing a more rapid decomposition of residual material in presence of aerobic bacteria.

Other miscellaneous chemicals and heavy metals reported by Hawkes and Anderson[3] for 20 Northern Great Plains coal strip mine ponds, with ranges of concentration (in mg/l), were aluminum 0-660, arsenic 1-4, cadmium 3-50, chromium 0-10, copper 1-22, iron

0-1100, lead 27-490, manganese 0-130, mercury 0-0.1, selenium 0-16, silica 100-19,000, and zinc 10-70.

Various theories on dissolved oxygen concentrations in strip mine ponds were reported by several workers. Simpson (1961) found that the concentration of dissolved oxygen in Kansas ponds was inversely related to water temperature and directly related to pH and photosynthetic rate of submerged plants. Tobaben (1969) and Coe and Schmelz (1972) reported lower oxygen concentration in young, highly acidic ponds; this was caused by the oxidation of dissolved sulfur or ferrous compounds. Coe and Schmelz (1972) stated that dissolved oxygen increases as oxidizable materials decrease and the density of phytoplankton and higher aquatic plants increases.

Dissolved oxygen concentration is important for respiratory processes in submerged vegetation and for emergents during winter when ice forms over the root crowns of shallowly submerged emergents. In cases where highly turbid water restricts light penetration and resulting photosynthetic processes, dissolved oxygen concentrations may become dangerously low from respiring flora and fauna without compensating photosynthetic production of oxygen. Resource managers may want to consider installing aerators on constructed impoundments over winter months to maintain dissolved oxygen concentrations.

In a western Maryland study, Davis (1971) reported that dissolved oxygen varies with depth and month. Burner and Leist (1953) found the lowest oxygen concentration in July and at the pond bottom on Kansas ponds. However, Lewis and Peters (1955) reported higher oxygen concentations at the bottom of southern Illinois ponds because extreme water clarity allows light penetration and corresponding rapid photosynthetic rates in submerged aquatic plants attached to the pond bottom.

Bell (1956) attributed high oxygen concentrations in both the epilimnion and hypolimnion of southern Illinois ponds to infertile water with a low biochemical demand for oxygen. He stated that high dissolved oxygen concentrations permitted *Typha* species to invade areas with water depths up to 60 cm. Sifton (1959) found that low oxygen concentrations are ideal for germination of *Typha latifolia* propagules; but once growth ensues, higher oxygen concentrations are required to meet increasing respiration rates. Linde et al. (1976) reported that *Typha* initially germinates in shallow water near shore and spreads to deeper water by vegetative propagation.

Crawford (1942) indicated that dissolved oxygen concentrations in central Missouri ponds are inversely related to the amount of organic matter on the pond bottom. Heavy decomposition of organic matter residue by anaerobic bacteria results in consumption and corresponding decrease in oxygen concentration and an increase in dissolved carbon dioxide (Burner and Leist 1953).

Hawkes (1978) reported that dissolved oxygen in Northern Great Plains coal strip mine ponds was near saturation and optimum for wetland vegetation due to wind action on water. Dissolved oxygen in 20 ponds he studied ranged from 5.9-20 mg/l with a mean of 9.3.

Crawford (1942) classified Missouri strip mine ponds into three types based on dissolved oxygen concentration. Oligotrophic ponds are rich in oxygen concentration at all levels with little deposition of organic matter and slow decomposition rates. Eutrophic ponds have low dissolved oxygen concentrations on the bottom, an abundance of dissolved nitrogenous substances, and rapid rates of decomposition with correspondingly high dissolved oxygen demand. Dystrophic ponds, characteristic of peat bogs, display extreme concentrations of nitrogenous compounds and organic acids. Oligotrophic ponds represent the best environmental conditions for wetland vegetation with respect to dissolved oxygen concentrations.

Water color and clarity in strip mine ponds has been discussed by several investigators. Tobaben (1969) reported alkaline lakes in Kansas to be greenish in color and acidic lakes blue-green in color due to the precipitation of colored organic matter. Crawford (1942) and Campbell and Lind (1969) found Missouri strip mine ponds deep reddish brown due to forms of dissolved iron. Parsons (1964) attributed turbidity of many strip mine ponds in Missouri to soluble ferric oxide concentrations. Bell (1956) concluded that in Illinois strip mine ponds ferric oxide acts as a filtering agent upon precipitation from basin water. Flocculation of negatively charged suspended soil particles with positively charged ions (sodium, potassium, calcium, and magnesium) results in a precipitate which settles to the bottom and promotes water clarity. Crawford (1942) stated that water clarity in the strip mine ponds he studied was due to the precipitate that forms when sulfuric acid flocculates with suspended materials.

Excessive water color can become a limiting factor for wetland plant establishment when light penetration and resulting photosynthesis is effected. However, in most cases light penetration is limited more by suspended solids rather than dissolved minerals. Precipitates formed by flocculation of suspended materials with oppositely charged ions can effect submerged vegetation by coating leaf surfaces and restricting photosynthesis. This can be an especially serious problem in deeper water where wave action is not present to remove precipitate material from submerged leaves (Emerson 1961).

The only information available on the water chemistry of stockdams comes from Hawkes and Anderson,[4] investigating nine livestock watering ponds on the Northern Great Plains. They found generally alkaline conditions in livestock watering ponds with pH values ranging from 6.8 to 10.3 . Specific conductance, a measure directly related to total filterable residues, was generally low with a range of 177-3100 umhos/cm. Salinities were not considered to be high enough to limit productivity on Northern Great Plains livestock watering ponds. Generally, these chemical parameters were well within acceptable levels for wetland plant development.

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[4] *Hawkes, C. L., and M. T. Anderson. Physical and chemical features of selected livestock ponds in the Northern Great Plains. (Unpublished manuscript at Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.)*

Among cations and anions, sulfate represented the highest concentrations followed by sodium with ranges of 28-924 and 8-602 mg/l, respectively. Other parameters were calcium 19-136 mg/l, magnesium 10-60 mg/l, potassium 10-23 mg/l, and chloride 2-19 mg/l.

Concentrations of organic macronutrients were high because of the large amount of aquatic vegetation associated with these livestock ponds. Total Kjeldahl nitrogen displayed the highest concentration, followed by total phosphorus and nitrate, with ranges of 0.27-2.63, 0.01-1.59, and 0-2.14 mg/l, respectively. Other miscellaneous chemicals and heavy metals reported by Hawkes and Anderson[4] for nine Northern Great Plains livestock ponds, with ranges of concentration (in mg/l), were aluminum 0-110, arsenic 1-13, cadmium 2-28, chromium 0-10, copper 1-9, iron 10-120, lead 22-350, manganese 0-3000, mercury 0-0.2, selenium 1-2, silica 400-14,000, and zinc 10-30.

Lathwell et al. (1969), working with artificial wildlife marshes in New York, reported trends in pH, carbonates, and dissolved oxygen. They found pH relatively stable diurnally and seasonally with values ranging from 8 to 10, well within acceptable pH range for the establishment of a variety of wetland vegetative types. Total alkalinity concentrations, a component of the carbonate system which provides a buffering effect under high acidity, influences toxic levels of dissolved heavy metals and the resulting wetland plant community composition. They noted that as alkalinity declined, heavy metal concentrations approached toxic levels for flora and fauna. Dissolved oxygen concentrations fluctuated substantially each day of the growing season. Lowest concentrations were observed in early morning hours when photosynthesis of aquatic plants was reduced.

As in strip mine ponds, chemical composition of water in natural wetlands is governed in part by the nature of the surrounding watershed (Moyle and Hotchkiss 1945, McCombie and Wile 1971). The extremely dynamic fluctuation of water levels in natural wetlands, caused mainly by evaporative loss and evapotranspiration during summer and spring runoff, is a major factor effecting the concentration of dissolved substances (Moyle 1945, Kadlec 1962, Rozkowska and Rozkowski 1969, Sloan 1970, Daborn 1976). Concentrations of dissolved substances are higher in low water levels typical at the end of the growing season and lower in higher water levels of early spring. In extremely dry summers, concentrations of dissolved substances may approach toxic levels for wetland vegetation in August and September. If possible, managers should consider adding water to wetland basins by midsummer if water regulation is available.

Moyle (1945) noted that presence of a white-powdered ring along shorelines or on mudflats indicates high salt content. Usually, wetlands with high salt content will support vegetation of high salt tolerance such as saltgrass (*Distichlis stricta*). As with strip mine ponds, the major cations in natural wetlands and lakes are calcium, magnesium, sodium, and potassium (Moyle 1945, Moyle and Hotchkiss 1945, Stewart and Kantrud 1972).

A characteristic of natural wetlands not found in strip mine ponds is the large amount of dead organic matter produced primarily from aquatic vegetation. Dineen (1953), Wilson (1958), Emerson (1961), Kadlec (1962), and Walker and Wehrhahn (1971) mention extremely low concentrations of dissolved oxygen and high carbon dioxide levels in basins with large amounts of organic matter. Rapid bacterial decomposition in warm, shallow water (utilizing large amounts of dissolved oxygen and producing high levels of carbon dioxide) overshadows the photosynthetic production of oxygen by aquatic plants. In restricted, shallow areas excessive oxygen consumption by bacterial decomposition could limit the amount of oxygen available for respiration by submerged vegetation, and result in a decrease of potential waterfowl food material.

Walker and Wehrhahn (1971) reported high levels of hydrogen sulfide in basins with high organic matter residue. Another characteristic of basins with high organic residue is the brownish water color from decomposition processes compared to greenish or blue-green color in strip mine ponds (Dineen 1953).

Water Temperature and Light Penetration

According to various workers, water temperature regimes were quite variable among strip mine ponds and natural wetlands. Crawford (1942), in central Missouri, reported that the highly acidic strip mine ponds he studied were not thermally stratified but stratification did occur in his eutrophic "control" ponds. Tobaben (1969) found only two of six study ponds in Pittsburgh, Kan., thermally stratified. Acidic ponds in his study area remained homothermous throughout the study period, which he attributed to high water clarity and a greater rate of thermal conductivity compared to alkaline ponds.

The effects of water temperature and thermal stratification on wetland vegetation are not known. Water temperature, however, is known to influence the time of germination in spring. Again, more research is needed to better understand the ecological relationship.

Lewis and Peters (1955) and Davis (1971) noted that their study ponds were thermally stratified, especially during June through October, with an abundance of oxygen in the lower thermocline and hypolimnion due to heavy plant growth on the pond bottom. Exceptional water clarity permitted good light penetration to photosynthesizing submerged vegetation. Burner and Leist (1953) and Simpson (1961) found no evidence of thermal stratification in their study ponds although changes in air temperature slightly effected surface water temperature. Parsons (1964) reported summer thermal stratification in reddish-black colored strip mine ponds; the stratification is caused by ferric iron oxides. Parsons (1964) encountered homothermous conditions in blue-colored ponds.

According to Crawford (1942), thermal stratification ı strip mine ponds is caused by a combination of epth, wind, isolation, and turbidity. Campbell and ind (1969) reported that seasonal water temperature eaches its maximum by July with the greatest rate f heat absorption in spring. Spring heat absorption riggers germination in aquatic plants.

Hawkes and Anderson,[4] studying nine livestock watering ponds on the Northern Great Plains, reported he absence of thermal stratification "due probably to hallow depths (maximum depth ranging between 1.7 nd 6.0 m) and the relatively constant prairie winds ocurring in the region". Water temperatures on their tudy ponds ranged from 2 to 27° C. Germination of vetland vegetation on shallow livestock ponds probıbly occurs earlier than deeper strip mine ponds due to nore rapid warming.

Much variation has been reported in water temperaure regimes on natural wetlands. In New York and Sasketchewan respectively, Emerson (1961) and Walker and Wehrhahn (1971) reported thermal stratification in natural wetlands with much colder temperaures in bottom water layers. Walker and Wehrhahn 1971) hypothesize that in many Sasketchewan wetlands there is continual upwelling of cold groundwater entering the wetland basin. Colder temperatures in bottom water layers may be beneficial to submerged vegetation since a higher level of dissolved oxygen generally occurs in colder waters. However, germination in spring could be delayed in comparison to warmer waters of shallow areas.

Dineen (1953) and Wilson (1958), both in Minnesota, and Daborn (1976), in western Canada, concluded that there was no thermal stratification in the shallow-water basins they studied. Smaller water volumes, characteristic of natural wetlands, result in a lower heat storage capacity and a rapid response of water temperature to fluctuating air temperatures (Daborn 1976).

Light penetration is another factor that effects aquatic plant growth by regulating photosynthesis and corresponding production of aquatic vegetation. Campbell and Lind (1969) found penetration to be greatest in slightly acid strip mine ponds but reduced in highly acidic and alkaline ponds, another possible explanation for reduced submergent vegetation on highly acidic strip mine ponds. In Kansas, Burner and Leist (1953) reported Secchi disc readings ranging from 60-225 cm in strip mine ponds. The depth of light penetration and resulting production of submergents corresponds directly to the concentration of dissolved solids (Beeton 1958, Emerson 1961, Coe and Schmelz 1972).

Hawkes (1978) reported secchi disc values of coal strip mine ponds on the Northern Great Plains to range from 0.4 to 4.4 m with a mean of 1.7, while livestock watering ponds ranged from 0.3 to 2 m with a mean of 0.8. He contends that the low secchi disc readings, indicating large concentrations of suspended particulate materials, may suggest lower production of phytoplankton and rooted aquatic vegetation caused by inhibited photosynthesis from reduced light penetration in the water column.

Death of aquatic plants, caused by precipitation of solids restricting light intensity on photosynthesizing leaves, is another complication associated with high concentrations of dissolved solids (Emerson 1961). Although not specifically mentioned by other authors, algal blooms may also contribute to lower aquatic vegetation production by restricting light penetration to photosynthesizing submerged plants and in some cases, excessive oxygen consumption for respiratory processes.

Soil Chemistry

Not much information is available on the soil chemistry of strip mine ponds. However, several investigators provide physical descriptions of both spoil pile material and submerged soil. In Ohio, Riley (1960) found the composition of surrounding spoil material to be 10% sand, sandy shale, and sandstone; 42% silty shales and loams; and 48% clay and limestone. He calculated that 4% of the spoil material was toxic to plant and animal life, 7% marginally toxic, 47% acidic but not necessarily toxic, and 42% calcareous. Bell (1956) found Illinois strip mine ponds to be primarily composed of calcareous shales. Parsons (1964) reported that 78% of spoil material in Missouri strip mine ponds was toxic to flora and fauna and pH values were commonly less than 4.0, seriously inhibiting vegetative development. Riley (1954) reported considerable variation in the pH of spoil material in Ohio. The common range was 4.5-6.5.

Bell (1956) and Brewer and Triner (1956) found Illinois spoil materials to be low in organic matter and nitrogen, a major nutrient for growing vegetation, but rich in potassium, phosphorus, and potash. Unlike other workers, Tobaben (1969) reported Kansas spoil piles to be well-vegetated with compacted soils and little erosion. He found that calcium was directly correlated with pH values.

Packer (1974) reported that soils west of the Missouri River in western North Dakota, eastern Montana, and Wyoming were deficient in phosphorus while soils in eastern North Dakota were deficient in nitrogen. In addition, sodium-toxicity problems are common in North Dakota spoil material because of the large amount of sodium associated with overburden of lignite coal beds. Sub-bituminous coal beds in eastern Montana and Wyoming have substantially less sodium concentrations and therefore no sodium-toxicity problems with respect to vegetative development.

Packer (1974) characterized spoil bank material in the Northern Great Plains as being "nearly always alkaline." Most spoil material in this region has a high saturation of clay and cation composition, which explains the high salinity levels found in most subsoils. Packer (1974) added that salinity problems can be corrected by introducing gypsum to subsoil material. However, this process is expensive.

In some areas of the Northern Great Plains, wind and water erosion of spoil bank material is a serious problem because of sandy soils which lack silt and clay for the formation of large aggregates. Some of the most highly erodible spoil material is found in North Dakota where sodium in clays and sandy soil predominate (Packer 1974). Constantly shifting spoil material from erosion processes hinders plant establishment, especially near shoreline where erodable materials enters the wetland basin.

Less is known about the submerged soils of strip mine ponds. Crawford (1942) described basin floors in Missouri, as a combination of gravel, shale, coal and sand mixed with dead vegetation. Closer to shore, Crawford (1942) found a shelf of soft, gray muck formed by flocculation of silty spoil material in the acidic pond water. Moyle and Hotchkiss (1945) reported that soft, mucky bottoms were unfavorable for many aquatic plants in Minnesota lakes. Riley (1960) found basin bottoms to vary from clays to clay, silty, or sandy shales; sandstones, and limestones.

There is no specific information available on soil characteristics for stockdams. However, Jupp and Spence (1977), working on Scottish lakes, in contrast to the findings of Moyle and Hotchkiss (1945) working in Minnesota, reported that vegetative growth is greater on fine-particle mud and clay bottoms than on coarse, gravelly bottoms. They concluded that fine-particle mud and clay bottoms, usually deposited in wind-sheltered areas, contain more nutrients than coarse-particle bottoms subjected to wind and subsequent wave action. Consequently, sheltered areas support more vegetative growth because of a higher nutrient status. Wilson (1937) stated that in Wisconsin lakes 88% of the plant biomass was found on organic soils, 22% on sand and silt bottoms, and no aquatic plants on pure gravel bottoms.

Resource managers, when anticipating construction of new impoundments, should consider wind-sheltered areas to reduce the erodibility of substrate from wave action. Wildlife, particularly waterfowl, also prefer wind-sheltered areas where an abundance of cover and food materials prevail.

Chemical features of natural wetland soils closely parallel soils of artificial wetlands, but some differences are apparent. Walker and Wehrhahn (1971) reported a thick layer of muck covering surface soils of Sasketchewan wetlands which results from large amounts of organic matter present on natural wetlands. This organic matter offers sufficient nutrients for plant growth as typified by generally greater vegetative development on natural wetlands.

Emerson (1961) highlighted the significant chemical features found in New York marshes. He recorded higher pH values in submerged soils because of ferrous, manganous, and ammonium hydroxides produced from anaerobic reducing conditions. The magnitude of total alkalinity, reflecting limestone content of the substrate and expressed as calcium carbonate, was directly correlated with the magnitude of nutrients essential for plant growth. Emerson (1961) concluded that alkalinity can act as an indicator of soil fertility. With regard to calcium, he found a direct correlation between soil calcium levels and pH. This is similar to the findings of Tobaben (1969) on Kansas spoil material.

Nitrogen, an essential element in plant growth, was found as the ammonium ion in submerged soil (converted by anaerobic bacteria) because conversion to nitrite and nitrate by aerobic bacteria cannot occur (Emerson 1961). However, when the soil dried, as on an exposed mudflat after drawdown, regular microbial nitrification processes proceeded under aerobic conditions and increased the availability of nitrogen for plant utilization (Emerson 1961, Kadlec 1962).

Harter (1966) stated that the main problems associated with nitrification processes in wet soils is the inhibition of aerobic bacterial action caused by the deficiency of oxygen. The amount of oxygen in soil is inversely proportional to water content. As soils change from dry, well-aerated to waterlogged conditions and vice versa, many bacterial decomposition processes are altered.

In many cases, the relationship between wetland vegetation and environmental factors on constructed impoundments is not known simply because of a lack of research information. The affects of environmental factors on the expression of wetland plant community development on constructed impoundments must first be understood before resource managers can devise management plans for these recently recognized ecosystems.

The need for additional ecological research on constructed impoundments is sufficiently warranted as demonstrated by our lack of information. Until more information is gathered, resource managers must extrapolate information from natural wetland studies to formulate management plans for these unique ecosystems.

Vegetation-Environmental Relationships

Specific floristic compositions have not been described for strip mine ponds or stockdams. However, general trends of vegetation development were indicated by some workers for strip mine ponds, stockdams, and natural wetlands.

Crawford (1942) found only a few species of aquatic plants distributed over Missouri strip mine ponds and no species in the most highly acidic ponds. He noted that more species occurred as water alkalinity increased. *Typha* species were the most common invaders. Crawford (1942) theorized that acidity and siltation are the main factors controlling biological processes in Missouri strip mine ponds. As acidity decreases and siltation increases, the diversity of organisms capable of existing increases, eventually modifying the habitat so conditions for plant invasion and establishment become more favorable. Riley (1960) reported that *Typha angustifolia*, *Typha latifolia*, and *Sagittaria cuneata* were the most abundant species of ascular plants in Ohio strip mine ponds. Lewis and eters (1955) and Bell (1956) found that the two earliest nvaders and most productive species in new strip mine onds in Illinois were *Typha latifolia* and *Potamogeton oliosus* (fig. 4).

Hawkes (1978) and Olson (1979) indicated that water urbidity and near-shore basin slope were major factors influencing biological processes in the Northern reat Plains. Highly turbid water, caused by suspended particulate material, limits light penetration nd associated photosynthetic activity in aquatic egetation. This is reflected in lower plant productivity nd lower invertebrate populations depending upon quatic vegetation for existence. Likewise, steep, nearshore basin slope limits the area favorable for aquatic lant community expansion and subsequently limits the otal biological productivity of that community. Acidity oes not appear to be a major problem effecting biological productivity in Northern Great Plains coal strip mine ponds since spoil material is generally alkaline in nature (Packer 1974, Hawkes 1978).

Walker and Wehrhahn (1971) commented on the complexity and variation in wetland vegetation occupying he glaciated prairie potholes. Auclair et al. (1973) discussed the mosaic pattern of nearly monospecific aquatic communities characteristic of natural wetlands. There is a strong tendency among emergent dominants o exclude each other.

Recently, considerable work has evolved around correlation of the distribution of aquatic macrophytes with environmental factors. A number of major environmental factors have been utilized to explain wetland plant distribution in strip mine ponds, artificial wetlands, lakes, and natural wetlands.

Crawford (1942), Burner and Leist (1953), Davis (1971), and Coe and Schmelz (1972) singled out basin slope as a major factor that effected plant distribution in strip mine ponds. They contend that the almost vertical position of the surrounding shoreline provides few shallow areas for production of aquatic vegetation and fish. Crawford (1942) and Coe and Schmelz (1972), adding water pH as another major factor, stated that steep shores, limited shoal areas, and high water acidity discourage invasion by aquatic plants. They concluded that shallow lakes are more productive because of enhanced exposure to light and air. Lewis and Peters (1955) and Bell (1956) found that fluctuating water levels and water pH were the major factors affecting plant distribution in Illinois strip mine ponds. They found that water level fluctuations beyond 1 m were not tolerated by *Typha* species. Riley (1960) stressed that flora density in Ohio, was determined by a complex set of factors including basin age, slope, water depth, water pH, soil fertility, and soil pH.

There is little information available which deals strictly with environmental-aquatic plant distribution relationships in stockdams. However, a few authors provided information for manipulation of aquatic vegetation to enhance waterfowl production in livestock watering ponds.

Several authors reported that waterfowl productivity increased when wetland vegetation was subjected to light or no grazing by domestic livestock. More attractive nesting and brood rearing cover was created

Figure 4.—Species of *Typha* are the earliest invaders of newly formed strip mine ponds and one of the most productive.

under restricted grazing. Berg (1956) found, in eastern Montana, that plant density, average plant height, and plant diversity increased in wetland plant communities fenced from grazing livestock. As a result, waterfowl nesting densities and brood production increased within fenced areas, especially on the larger reservoirs. Lokemoen (1973) reported that in western North Dakota, reduced grazing pressure improved waterfowl habitat through enhanced wetland plant development. Breeding pairs were significantly more numerous on lightly grazed ponds with grassy shorelines while broods were more numerous on ponds with brushy shorelines of emergent vegetation.

Evans and Kerbs (1977) reported that, in western South Dakota, rapidly changing water levels, light livestock grazing pressure, and gently sloping shorelines encouraged greater waterfowl nesting and brood use on stockdams through the enhancement of wetland plant communities. They noted that grazing had a considerable impact on the wetland vegetation around stockdams. In a similar study in south central South Dakota, Rumble (1979) found that excessive grazing of shoreline vegetation reduced the number of waterfowl broods using a pond. He concluded that excessive grazing and trampling of wetland vegetation increased pond turbidity and reduced biological productivity.

Dane (1959) and Lathwell et al. (1969), working with artificial wetlands in New York, indicated that basin slope is an important factor in plant distribution. Lathwell et al. (1969) stated that greater plant growth occurred in shallow basins, but indicated that specific factors controlling production in wetlands were not known. Dane (1959) reported that species composition of wetland plant communities was governed by basin slope, nature of the bottom soils, water clarity, depth, and extent of water level fluctuation. He concluded that the more gently sloping basins were characterized by wider zones of wetland vegetation (fig. 5).

Moyle (1945, 1956), Moyle and Hotchkiss (1945), Sculthorpe (1967), and Modlin (1970) indicated that plant distribution in lakes is dependent on water quality, bottom soil texture, and bottom soil fertility. Another major factor that often effected plant density was the amount of light penetration reaching submerged aquatics. As water depth and turbidity increase, the amount and depth of light penetration decreases (Juday 1934, Robel 1961, Spence and Chrystal 1970). Spence and Chrystal (1970) concluded that light penetration is as important as substrate factors or intraspecific competition in influencing plant establishment. Natelson (1954) and Swindale and Curtis (1957), working with submergents found water chemistry, depth, and substrate fertility important in Wisconsin lakes. Jupp and Spence (1977) reported that *Potamogeton filiformis* and *Potamogeton pectinatus* were limited by wave action and waterfowl grazing. They claimed that waves reduced plant biomass directly in exposed areas and indirectly by creating coarse, nutrient-poor bottom soils.

Features of the bottom substrate were often discussed as factors that effected plant establishment. Pearsall (1926), Wilson (1937), and Misra (1938) mentioned substrate fertility as the prime factor determining establishment. In a California study, Mall (1969)

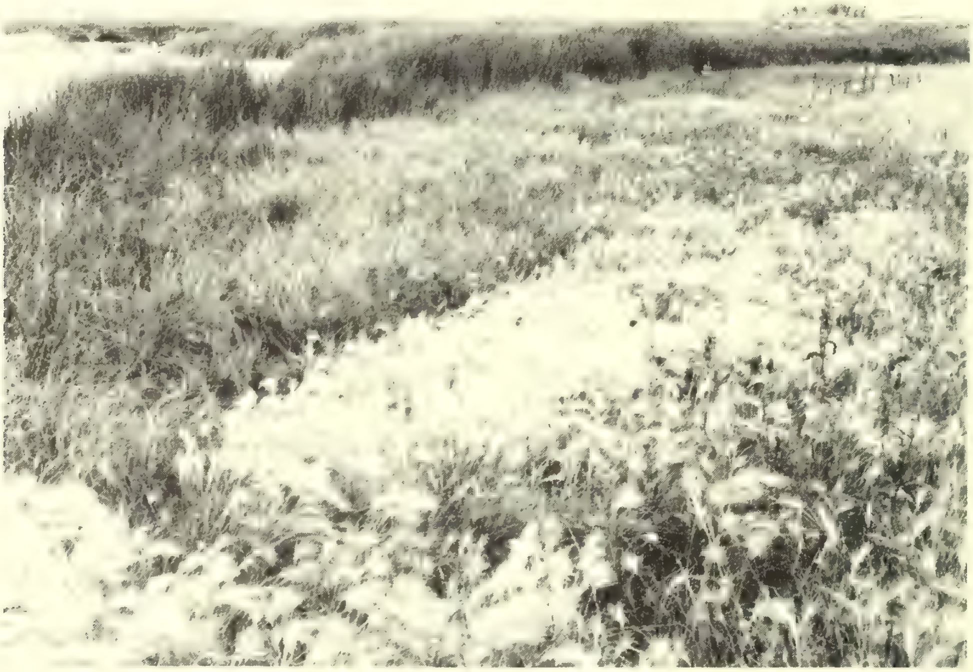

Figure 5.—Natural wetlands and stockdams with gently sloping basins, pronounced water-level fluctuations, and average water pH display wider, more developed zones of wetland vegetation.

ncluded that the length of soil submergence is most nportant, followed by levels of soil salinity. Veatch 932) discovered the most prolific growth of aquatic lants on soft, slimy, sedimentary peat or organic mud ottoms and reduced growth on nearly pure sand, cobles, or hard rock in Michigan. Water level fluctuaons were also mentioned as prime factors (Graham nd Henry 1933, Potzger and Van Engel 1942, Mandos-ian and McIntosh 1960). Potzger and Van Engel (1942) ncluded physical factors of the substrate (soil texture, ave action causing coarse soils, and slope) as factors at effected plant establishment. Mandossian and cIntosh (1960) and van der Valk and Bliss (1971) dis-ussed chemical characteristics of the water in addiion to fluctuating water levels. Zutshi (1975) stated hat prolific growth of aquatic plants was associated ith shallow water, rich organic soils, and little wave ction.

Many investigators working with natural wetlands ave found that water depth and permanence influ-nces the establishment of wetland plant communities Kadlec 1962, Harter 1966, Millar 1969a, Smith 1969, uclair et al. 1973). Studying in North Dakota, Stewart nd Kantrud (1972) found a definite association of pecific plant species with differing water permanence not depth) and specific conductance of surface waters. Walker and Coupland (1968), Walker and Wehrhahn (1971), and Dirschl and Coupland (1972) reported that disturbance, soil fertility, water regime, and salinity account for the bulk of variation in the characteristics of plant communities in Canadian wetlands. Emerson (1961) divided the major factors influencing plant establishment into chemical features (soil pH, soil fertility) and physical features (slope, water depth, hardness of the bottom). He reported that wetlands with steep slopes had narrow emergent zones with sparse vegetation development. Auclair et al. (1976a, 1976b) believed that soil fertility was the sole factor in plant establishment and growth.

Several workers have reported on the practical aspect of fluctuating water levels and deliberately manipulated levels for selecting and managing specific plant communites (Schmidt 1951, Johnsgard 1956, Kadlec 1962, Robel 1962, Harris and Marshall 1963, Anderson and Glover 1967, Burgess 1969, Meeks 1969). Drawdowns provide several advantages for wetland plant communities. They (1) allow a greater rate of organic matter decomposition under aerobic conditions with a subsequent release of nutrients into the mudflat, (2) favor germination of aquatic plant seeds and subsequent development of lush emergent cover, and (3) enhance the availability of aquatic plant seeds to feeding waterfowl (Kadlec 1962). Interspecific competition, soil chemical characteristics, the rate at which soils dry after drawdown, water depth after flooding, and seed availability all interact to influence which aquatic plants will invade an exposed mudflat (Meeks 1969).

Pond age, another variable which could effect the development of wetland plant communities in strip mine ponds, was found to be insignificant in Illinois ponds (Lewis and Peters 1955). They concluded that the nature of spoil material is more important than age in determining chemical characteristics of pond water and eventual establishment of aquatic plants.

In the Northern Great Plains, the influence of pond age on wetland plant establishment and development is still unknown (Hawkes 1978 Olson 1979). It has been suggested that the chemical moderation of spoil bank material over time, a corollary process associated with age, is more important than pond age in influencing wetland plant development.

Summary

As strip mining and stockdam construction accelerate in the Northern Great Plains, resource managers must develop more intensive management plans for these specialized ecosystems. As indicated by the current literature, there is little ecological information available, and only limited future research interest exists for these rangeland ecosystems. More information is needed on the ecology and biology of both flora and fauna of these ecosystems.

We must realize the additional potential assets offered by managing wetland vegetation on these rangeland impoundments. With proper management, we can convert these ecosystems into functional multiple use areas.

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Water regime, chemical features, temperature factors, light penetration, substrate properties, and physical characteristics are described for Northern Great Plains strip mine ponds and stockdams, followed by a discussion of how their interaction determines wetland plant community composition and resulting wildlife habitat quality for consumptive and non-consumptive resource utilization.

Keywords: Strip mine ponds, stockdams, wetland management, wetland wildlife habitat, wetland vegetation ecosystems

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Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

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Pine and Juniper Diseases in the Great Plains

Glenn W. Peterson

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Abstract

The results of research on diseases of pines and junipers in the Great Plains are presented; diagnosis, biology, damage and control are emphasized.

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Pine and Juniper Diseases in the Great Plains

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Pine and Juniper Diseases in the Great Plains

Glenn W. Peterson

Introduction

Pines and junipers are widely used in windbreak, shelterbelt, park, landscape, Christmas tree, roadside, wildlife, and other types of plantings in the Great Plains. The pines and junipers are especially valuable in plantings established for the protection of soil, crops, livestock, wildlife, and dwellings, because they provide protection all year.

Research on a number of diseases of pines and junipers throughout the Great Plains has been conducted since 1958 by the USDA Forest Service's tree disease project in Lincoln, Nebr., in cooperation with the Nebraska Agricultural Experiment Station. This publication summarizes the major results of the research.

Emphasis has been placed on results which pertain to diagnosing the diseases and controlling them. The first sections under each disease cover damage, geographic distribution, trees affected, and control. This information is included primarily for those who need to apply the information in the field. The last section under each disease is devoted to physiological and morphological information on the pathogens. Such information is included for researchers and other specialists who will be working with the pathogens in laboratories, greenhouses, and growth chambers.

1. Dothistroma Needle Blight of Pines

Pines affected by Dothistroma blight lose needles prematurely, thereby reducing growth. Repeated attacks sometimes kill trees. The infected needles become discolored (brown) prior to being cast. Some of the discolored needles remain on trees for months, thereby destroying the esthetic value of pines in landscapes and making Christmas trees unmarketable (fig. 1-1).

Dothistroma pini, the fungus causing this blight, affects several pine species in 21 states in the United States, including southeastern Alaska (fig. 1-2). Ponderosa and Austrian pines, which are highly susceptible, have been severely damaged in the Great Plains. Scots pine is highly resistant to *D. pini*. This fungus is present in some natural pine stands, but it causes more damage to planted pines. In the Great Plains, the disease is encountered in windbreaks, and Christmas tree, roadside, park and other plantings.

Diagnosis

Symptoms of Dothistroma blight in the central United States develop in the fall of the year of infection. Usually, infection is more intense in the lower crown of trees (fig. 1-3), but the entire crown can be infected (fig. 1-1), even in 35-year-old trees.

Early symptoms on needles consist of deep green bands (fig. 1-4) and yellow and tan spots. The spots and bands may turn brown to reddish-brown (fig. 1-5). The reddish bands are more distinctive and numerous on infected pines in the western United States (California, Oregon, Washington, Idaho) where this disease is often referred to as the "red band" disease.

Commonly, the ends of infected needles turn light green, then yellow, and then necrotic (brown), with the base of the needles remaining green (fig. 1-6). Needles may develop extensive necrosis (browning) 2 to 3 weeks after the symptoms first appear.

Spores of the fungus are borne in fruiting bodies, which develop below the epidermis of needles. The fruiting bodies develop in lesions (fig. 1-7). As the fruiting bodies enlarge, they split the epidermis longitudinally along two sides of the fruiting body (figs. 1-8, 1-9). The earliest developing fruiting bodies are frequently located near the margin between brown and green tissues (fig. 1-10). In the central United States, these fruiting bodies may enlarge sufficiently in late fall to split the epidermis. They generally do not mature and produce spores until the following spring, however.

Infected needles drop prematurely. Infected second-year needles are cast before infected first-year (current-year) needles. In some years, second-year needles are cast in late fall of the year they become infected. In other years, loss of needles is not extensive until late the following spring or early summer. Needles that become infected the year they emerge often are not shed until late summer the following year.

In the central United States, trees may become infected from May to October. Although infection can occur early in the growing season, symptoms do not develop before September. Symptom development is usually not extensive until November or December.

Damage caused by *D. pini* may be confused with damage from other causes. Pines under moisture stress frequently have needles with brown tips. The brown tips of such needles are usually severely constricted, whereas tips of Dothistroma-infected needles are only slightly constricted. The demarcation between discolored tips and green tissue is sharp in Dothistroma-infected needles, but is gradual in needles under moisture stress.

Needles damaged mechanically, such as by spray or cultivation equipment, may have bands, spots, and brown tips. Similar damage can be caused by some insects. Dothistroma may be distinguished from such damage by the presence of fruiting bodies. These dark-colored bodies can be seen in the spots and bands.

It may be difficult to distinguish Dothistroma blight from brown-spot needle blight caused by the fungus *Scirrhia acicola*. The symptoms of these two diseases are similar. Both cause spots, bands, and dead needle tips. Symptoms of brown spot develop earlier than symptoms of Dothistroma. Symptoms of brown spot were observed in July, in eastern Nebraska, in 1971, when Dothistroma symptoms were not evident before October. These two fungi are best distinguished by differences in their spores. Both fungi produce long cylindrical conidia (spores) which have from 1 to 5 cross walls (septations); however, *D. pini* conidia are transparent (hyaline), whereas *S. acicola* conidia are greenish-brown. There are also differences in size of conidia of the two fungi. A specialist may have to be consulted to make the distinction.

Life Cycle

Spores of *D. pini* are dispersed from May to October, in the central United States (figs. 1-11, 1-12). The spores are dispersed primarily by rain splash and, therefore, are not dispersed long distances. Spores deposited on needles germinate when temperature and moisture conditions are favorable. The spores produce germ tubes which grow in a positive direction toward stomates through which they enter needles (figs. 1-13, 1-14, 1-15).

Second-year and older needles of ponderosa and Austrian pines are susceptible from late May through the growing season in the central United States. However, first-year (current-year) needles of these two pines are not susceptible until mid-July. Fruiting bodies of the fungus develop after symptoms appear. In the central United States, spores are rarely formed in the fall of the year of infection. Spores which are formed in the fall do not cause infection in the fall, because conditions at that time are not favorable for infection. In the following spring, fruiting bodies mature and spores develop within them. These spores then initiate new infections, and the disease cycle is repeated.

Dothistroma pini is spread to new areas, in most cases, by infected nursery stock. There is considerable evidence that the fungus is spread by distribution of 1- to 3-year-old seedlings. Infection in stock this age is often low and difficult to detect. A survey of 60 Christmas tree plantings in Nebraska revealed that half of the plantings contained Dothistroma-infected trees. Because these plantings were located far from other pines, planting stock appears to be the source of infection. Infection in some planting stock was so low that growers were not aware of blight in their plantations until 4 or 5 years after planting. It is unlikely that long distance spread is caused by spores being carried by wind from infected trees to new plantings. In eastern Nebraska no infection has occurred in a ponderosa pine planting located 1 km from an Austrian pine plantation that has been severely infected since 1967.

Control

Dothistroma pini can be controlled by proper timing of fungicide treatments, just before the period of susceptibility (fig. 1-16). Because second-year and older needles of Austrian and ponderosa pines are susceptible in late May, fungicide applied in mid-May will protect these older needles. Fungicide applied in mid-May will not protect new needles, however, because at that time they are very small (just emerging from fascicle sheaths). New needles of Austrian and ponderosa pines do not have to be covered with fungicides early in the season because they are not susceptible until mid-July (fig. 1-16). A second application of fungicide in mid-June will effectively protect new needles.

There is a low risk in using just one fungicide application. Results from research in eastern Nebraska show that one application in mid-June will provide satisfactory control in most years, although older needles will be unprotected for a short period (late May to mid-June). In eastern Nebraska, initial infection did not occur until about mid-June in four out of five years. Many Christmas tree growers in the central United States are effectively controlling Dothistroma with a single fungicide application.

Annual spraying for control of *Dothistroma pini* is unnecessary in certain types of plantings. Because essentially complete control of this pathogen can be obtained with fungicides, managers can risk not spraying every year in park, residential, and similar types of plantings. If infection occurs during the year in which fungicide is not applied, fungicide can be applied the next year, knowing good control will be obtained. If no or little infection occurs the year skipped, then another year can be skipped. However, Christmas tree growers probably should not skip any years because of the possibility of high financial loss.

Copper fungicides prevent infection by *D. pini*. Bordeaux mixture (8 pounds of copper sulfate, 8 pounds of hydrated lime, and 100 gallons of water) is very effective and is registered for control of Dothistroma. Fungicides containing copper salts of fatty and rosin acids are also registered for Dothistroma control.

The impact of *D. pini* can be reduced by use of resistant trees. Pine species differ in resistance to *D. pini*. Scots and red pines are highly resistant, whereas ponderosa and Austrian pines are highly susceptible (fig. 1-17).

Resistance to the fungus varies considerably within species. An evaluation of 22 geographic sources of *Pinus nigra* revealed that some trees from 16 of the sources had high resistance; all trees of one geographic source had high resistance (fig 1-18). Seedlings are now being produced in the Great Plains from seed collected in an area in Yugoslavia where the resistant trees originated. Resistance to Dothistroma is being evaluated in 50 geographic sources of ponderosa pine in eastern Nebraska.

The pattern of resistance varies considerably in Austrian and ponderosa pines. On some trees, needles of all ages are highly resistant. On other trees, current-year needles are resistant, but older needles are susceptible (fig. 1-19).

Physiology and Morphology

The fungus has both a sexual stage (*Scirrhia pini*) and an asexual stage (*Dothistroma pini*). The sexual stage has been found in British Columbia, Alaska, Oregon, and California but not elsewhere in North America. Ascospores are produced by the sexual stage; their role in development of epidemics is not known. Conidia (spores produced by the asexual stage) are cylindrical, curved, 1- to 5-septate but usually 3-septate, and hyaline (fig. 1-11). The conidia from the central United States are considerably shorter on the average than those found in the western United States. The average dimensions of conidia in seven separate collections from Nebraska were 21.3 μm × 2.5 μm.

Conidia from Nebraska collections germinated over the temperature range 12-28°C when incubated on water agar. Conidia incubated on water agar had optimum germination at 24°C (fig. 1-20). Germination was near optimum at 22°C but dropped off rapidly below 22°C and above 24°C. Germ tube growth on water agar was optimum at 22-24°C (fig. 1-20).

Conidia incubated in water had optimum germination at 22-24°C; germ tube growth was optimum at 24°C. Germ tubes growing in water at 22°C and 26°C were markedly shorter than those at 24°C.

Conidia incubated on water agar germinated earlier than conidia incubated in water; germ tubes grew faster on water agar. At 24°C conidia on water agar started to germinate between 6 and 8 hours after incubation started (fig. 1-21), whereas conidia in water started to germinate between 8 and 10 hours after incubation started. These results show that when comparing germination of *D. pini* conidia from different collections, results can be obtained quicker if spores are germinated on water agar rather than in water.

The optimum temperature for germination of *D. pini* conidia has been reported to be near 18°C in New Zealand and in Kenya. The germination tests in these countries involved incubation in water, whereas, in the Great Plains, conidia were incubated on water agar. To see if methods might account for the differences, 10 isolates were incubated on both water agar and in water. Because the optima were similar in water and on water agar, the difference in optima are likely real and not a result of differences in germination test methods. Accordingly, there is a possibility that the lower temperature (18°C) for optimum germination of conidia in New Zealand and Kenya results in more infection at lower temperatures in those countries than in the central United States, where the optimum for germination is 24°C.

Growth of the fungus on malt extract agar was best at 20°C; growth was moderately good at 16°, 22°, and 24°C.

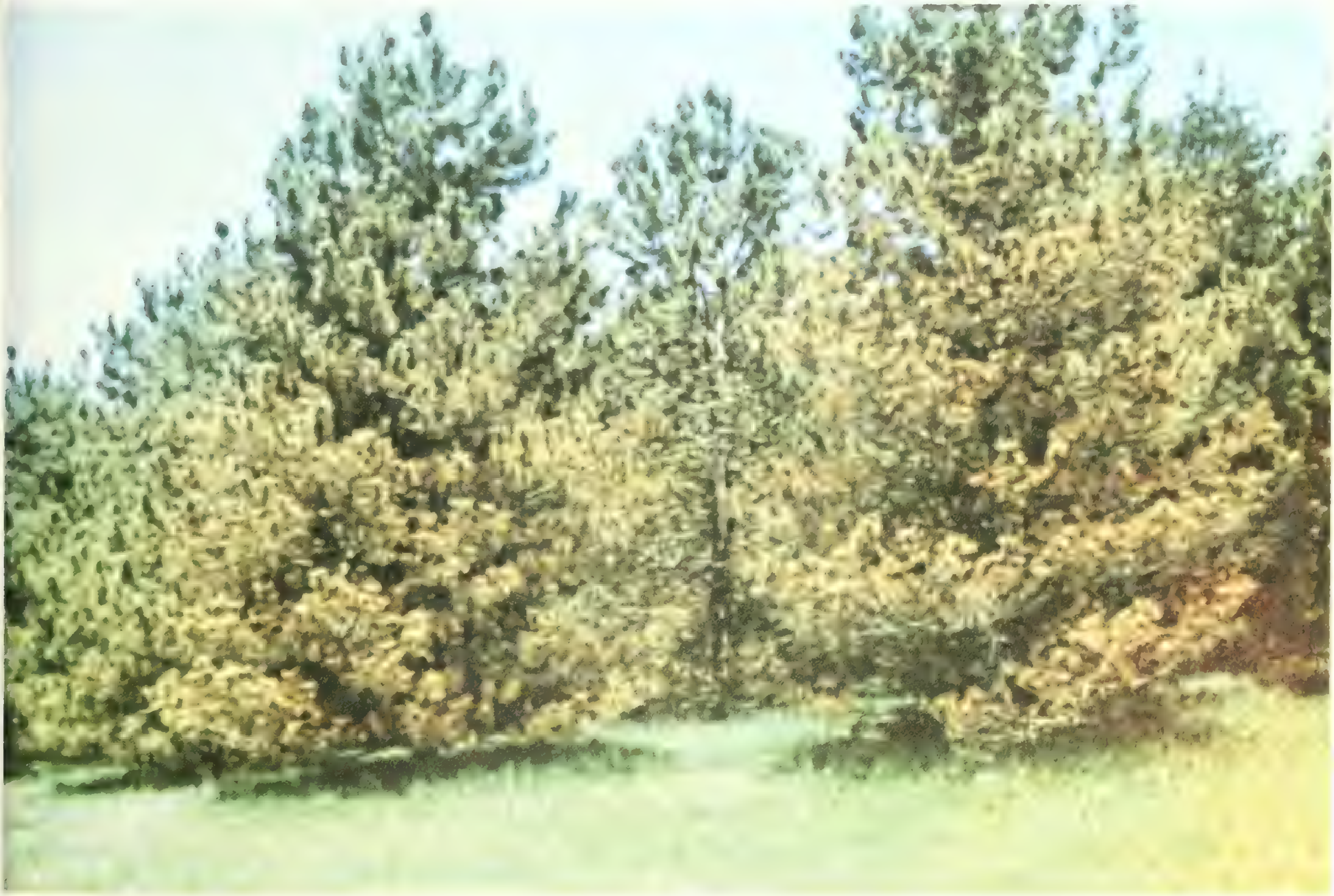


Figure 1-1.—Austrian pines infected by *Dothistroma pini*.

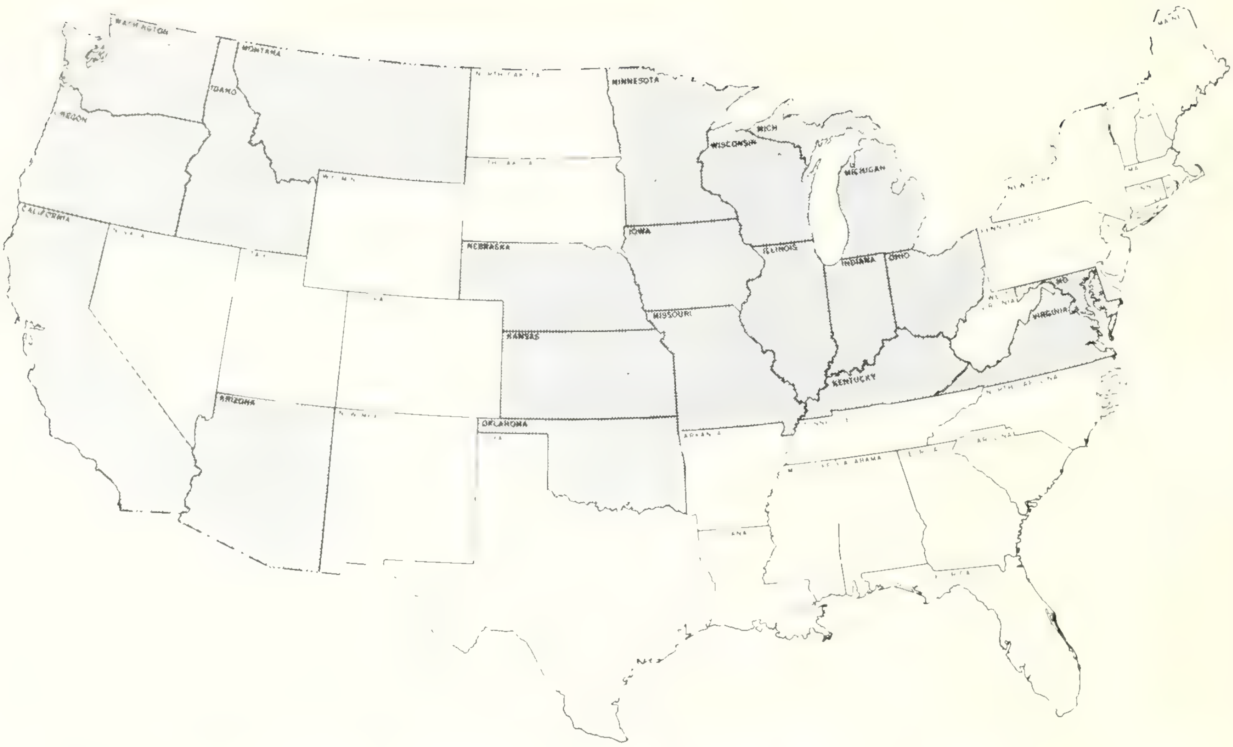


Figure 1-2.—*Dothistroma pini* occurs in shaded states and in southeastern Alaska.

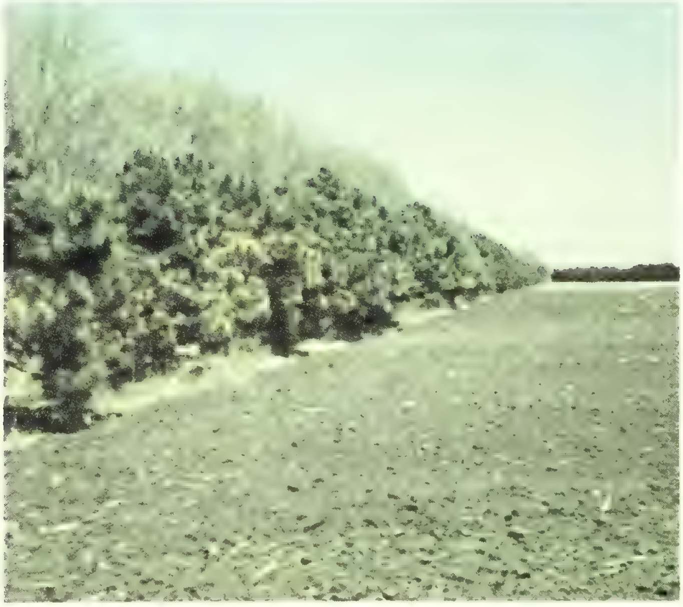


Figure 1-3.—Infection of the lower crowns of ponderosa pines in a field windbreak.

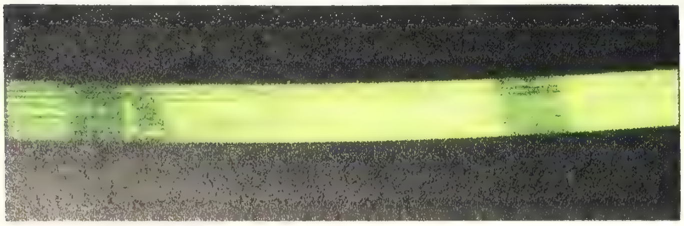


Figure 1-4.—Early symptoms of Dothistroma blight—deep green bands.

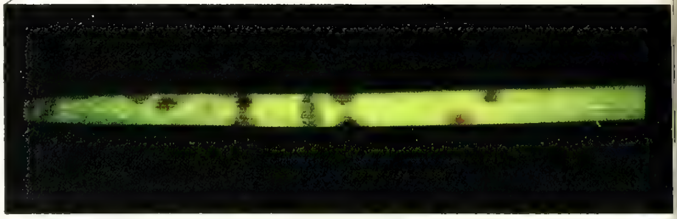


Figure 1-5.—Typical symptoms of Dothistroma blight—reddish brown spots and bands.

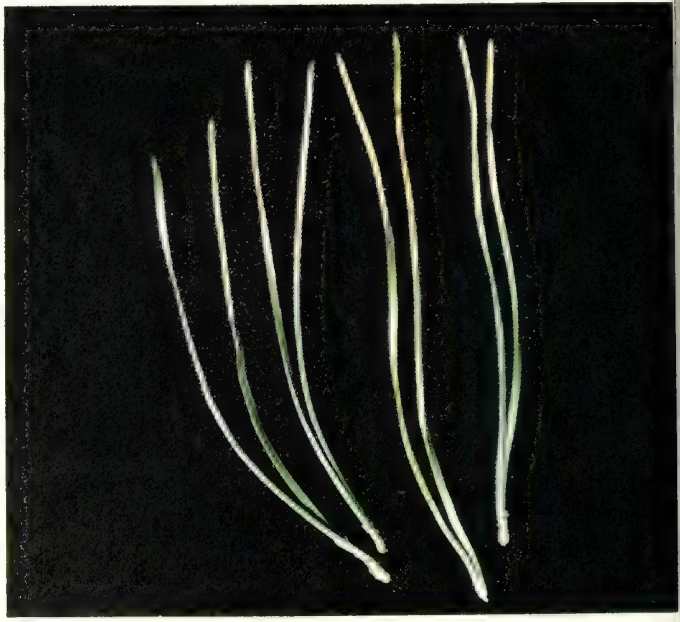
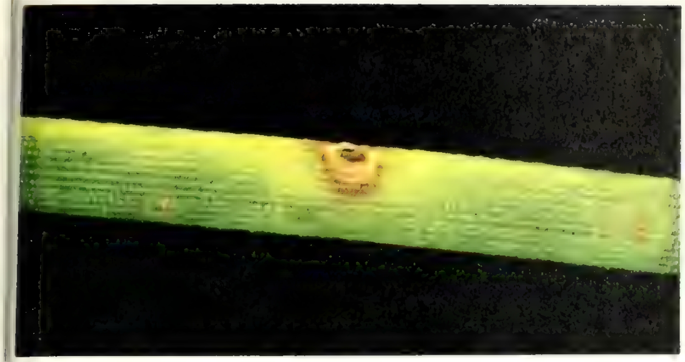


Figure 1-6.—Symptoms typical of *Dothistroma pini* infected needles—tips brown, bases green.



igure 1-7.—Lesion on infected needle with an erumpent fruiting body of *Dothistroma pini.*

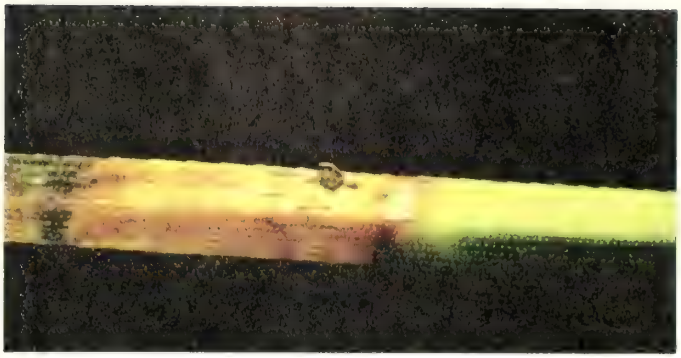


Figure 1-10.—Erumpent fruiting body of *Dothistroma pini* located near margin between brown and green tissues.

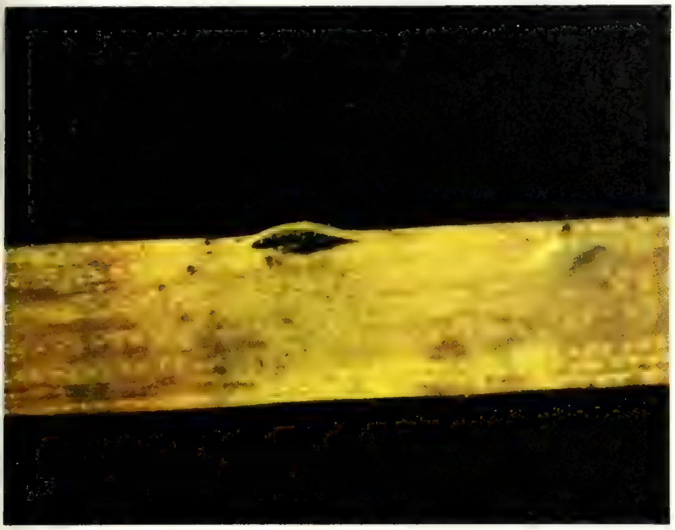


Figure 1-8.—Needle epidermis split and raised by developing fruiting body of *Dothistroma pini.*

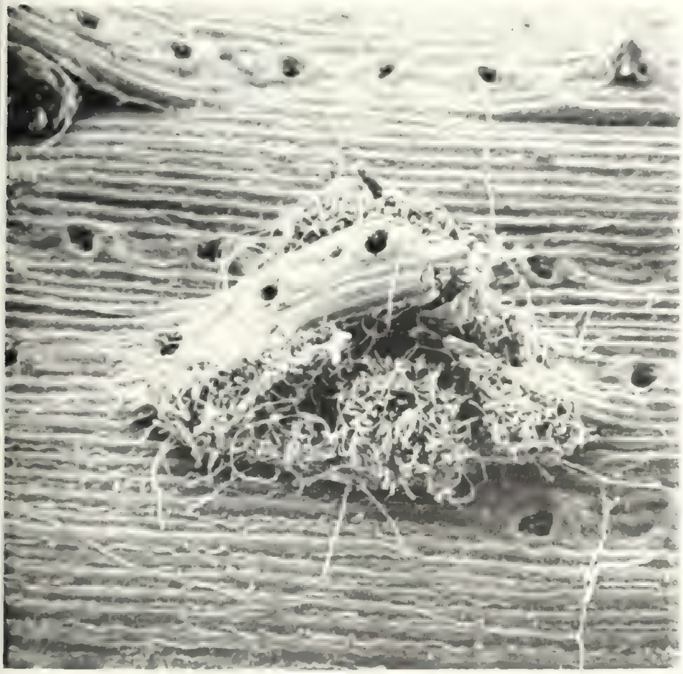


Figure 1-9.—Flap of split epidermis raised by *Dothistroma pini* fruiting body. (X200)

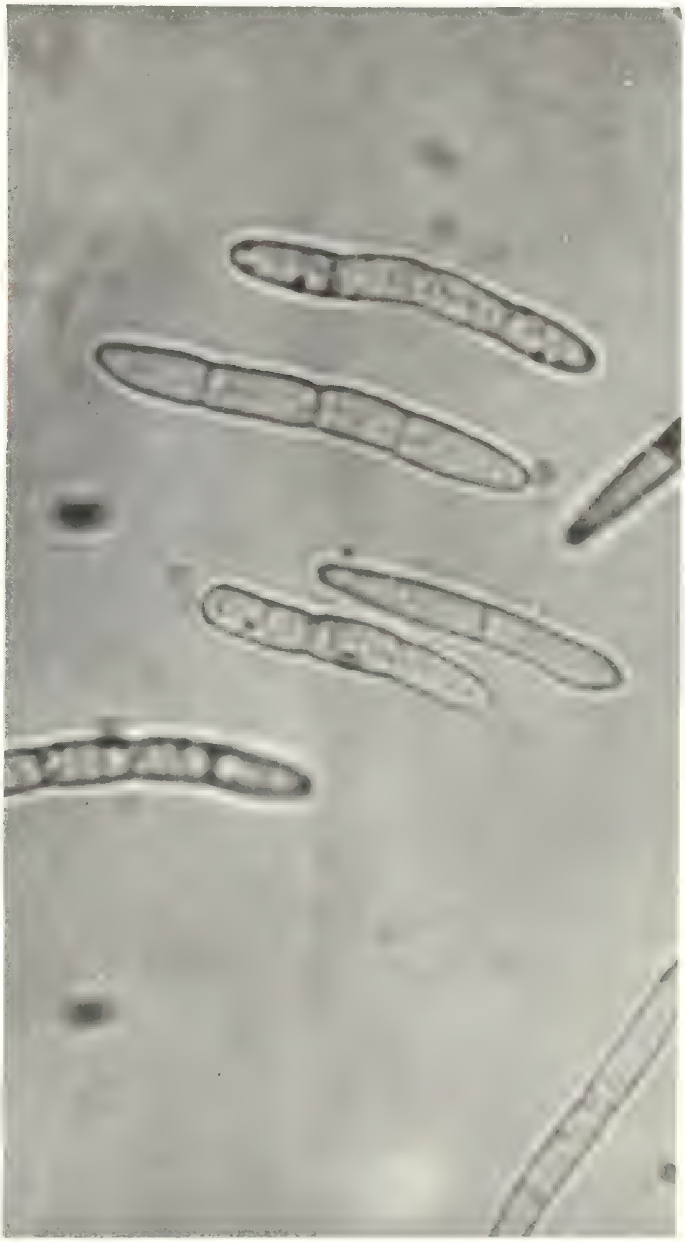


Figure 1-11.—Conidia of *Dothistroma pini,* stained with cotton blue to show cross walls.

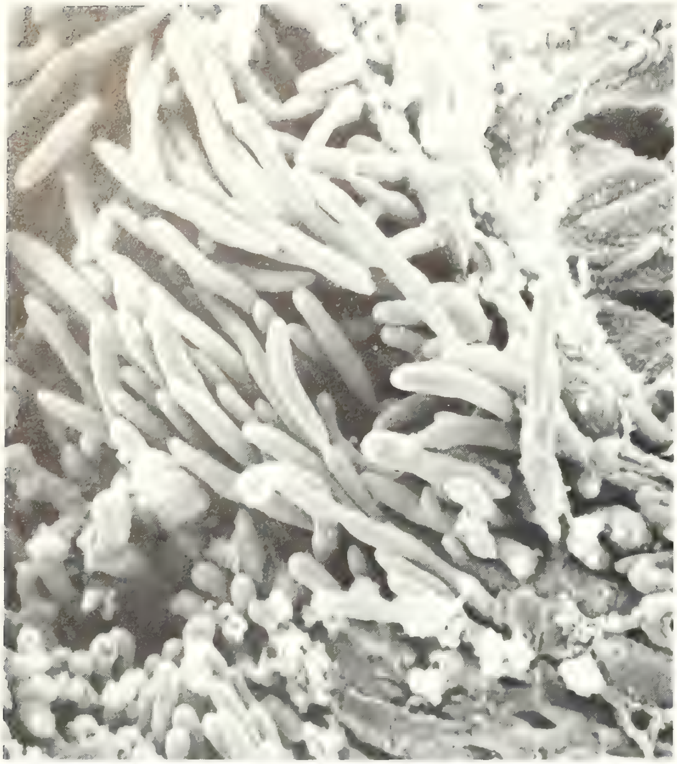


Figure 1-12.—Spores (conidia) of *Dothistroma pini.* (X2000)

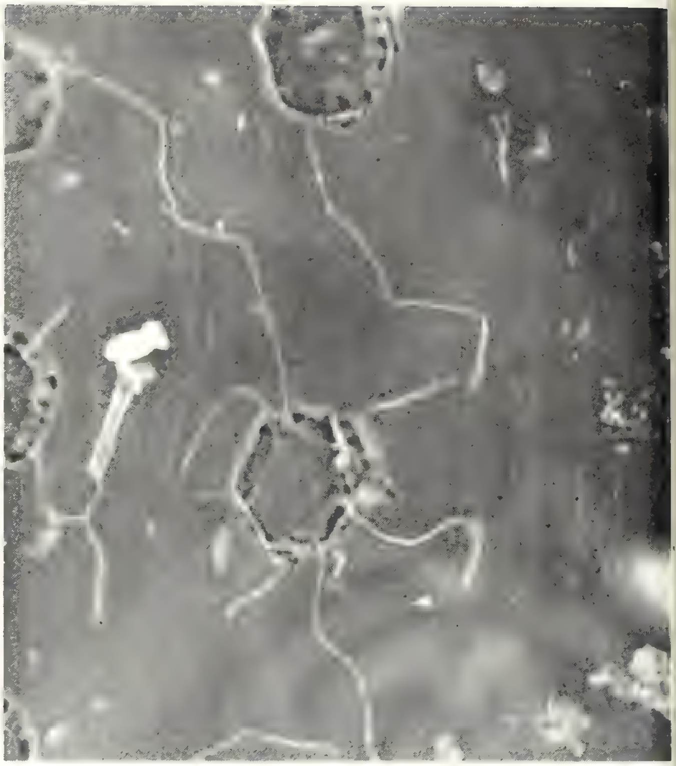


Figure 1-14.—Germ tubes from several conidia of *Dothistroma pini* growing in a positive direction toward stomates, on an Austrian pine needle collected in the field.

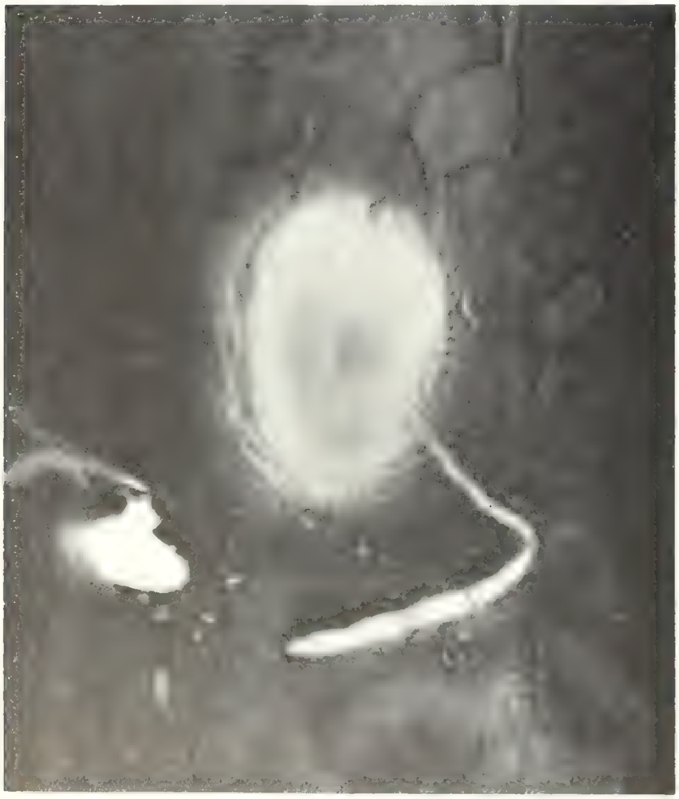


Figure 1-13.—Germinated conidium of *Dothistroma pini* with germ tube growing toward a stomate, on an Austrian pine needle.

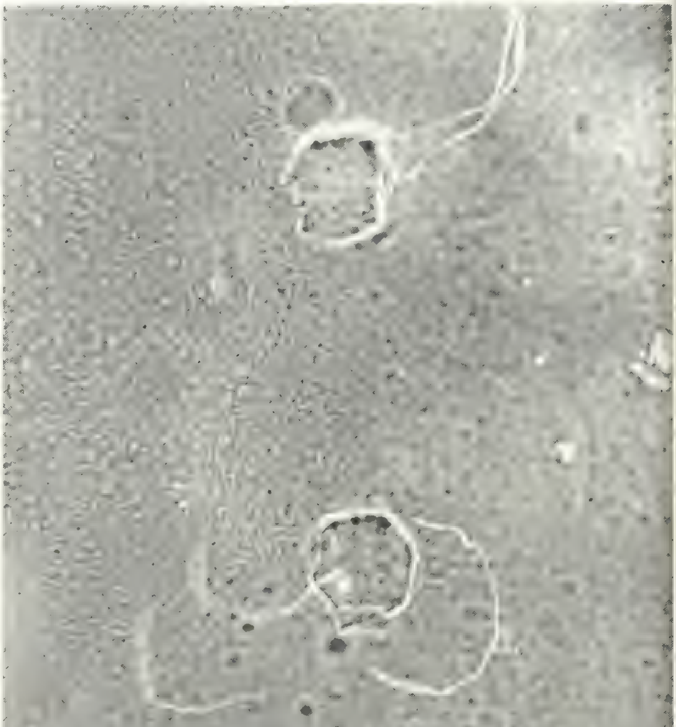


Figure 1-15.—Germ tubes of *Dothistroma pini* curving towards stomates on an Austrian pine needle.

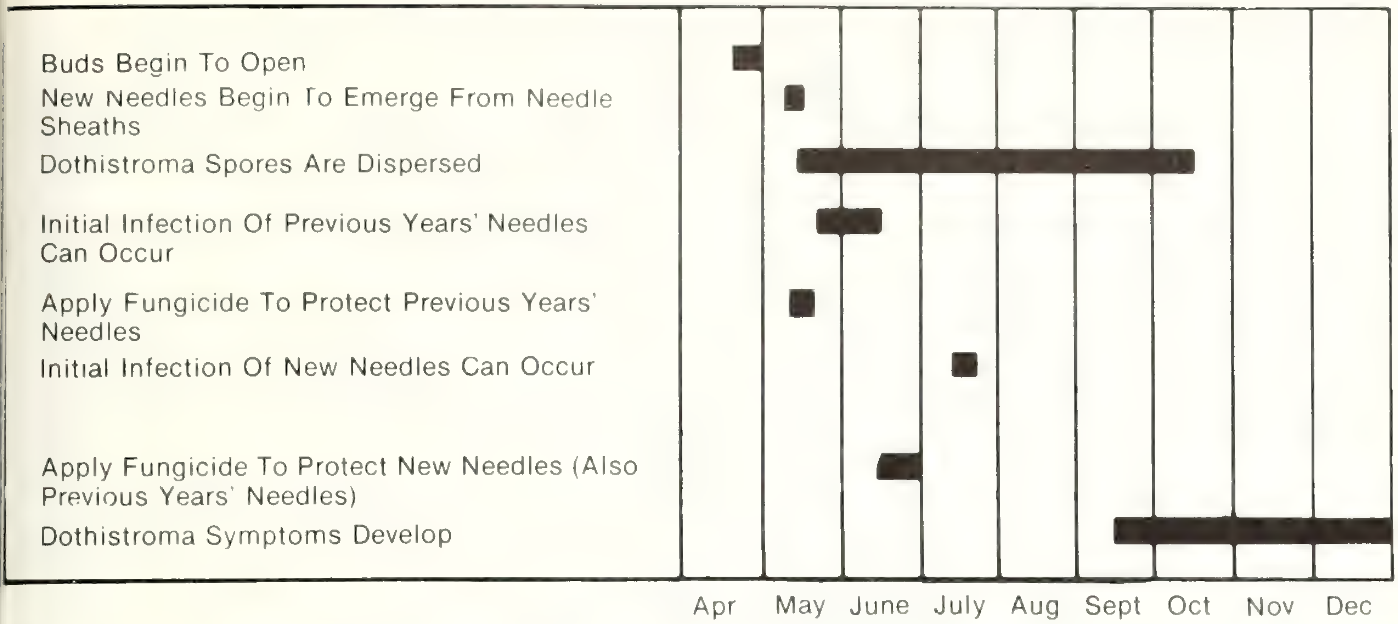


Figure 1-16.—Schedule for developing programs for control of Dothistroma blight.

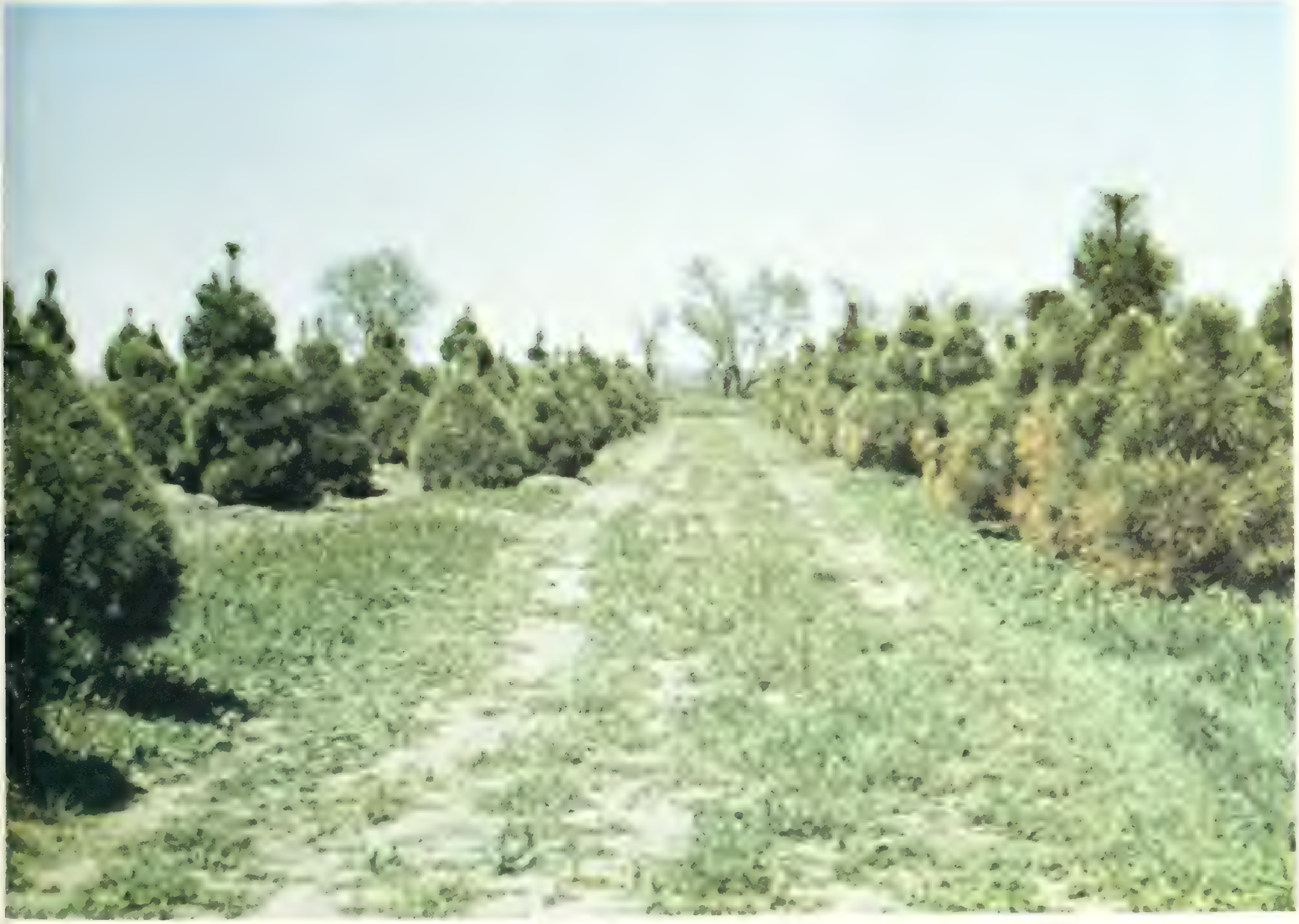


Figure 1-17.—Resistant Scots pines (left) adjacent to susceptible Austrian pines (right).

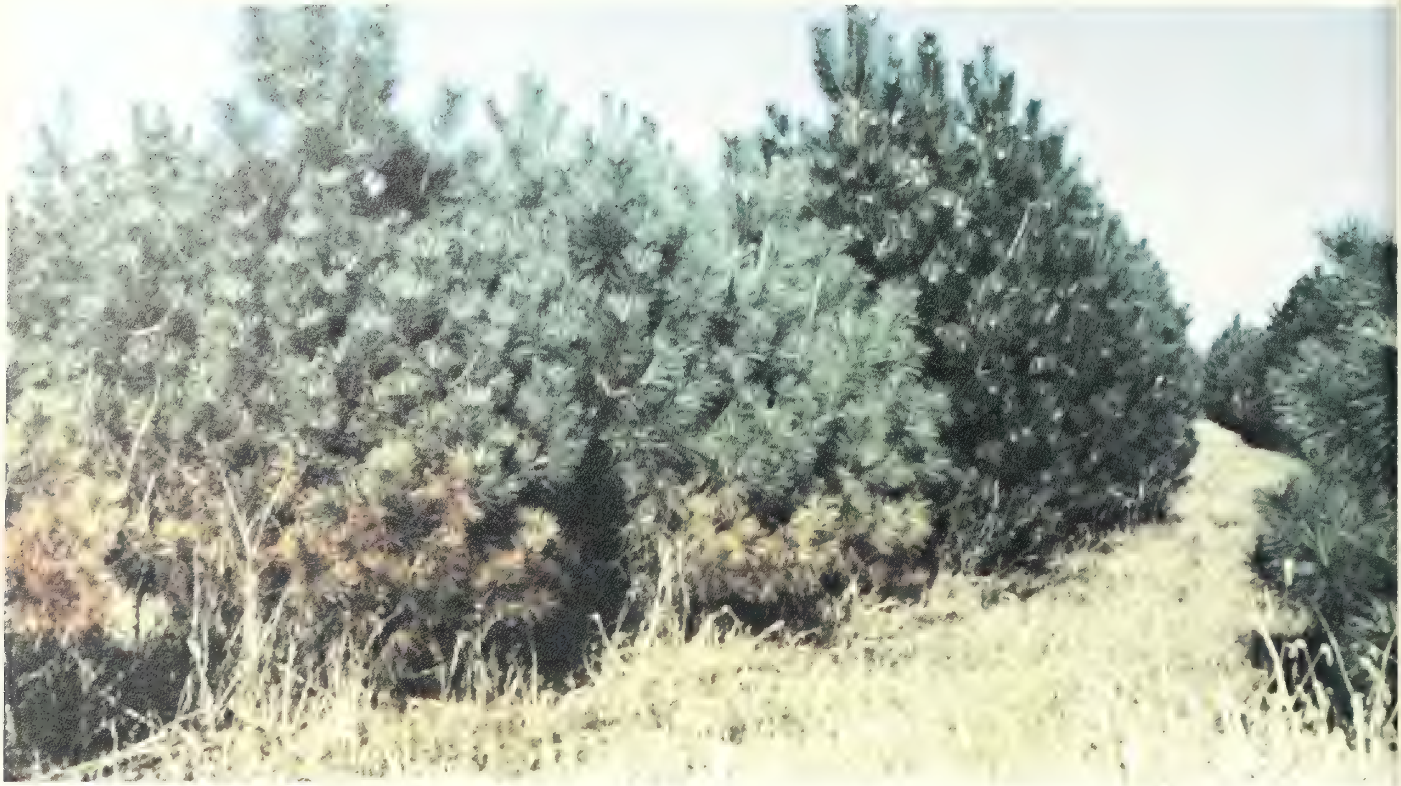


Figure 1-18.—A Yugoslavian source of *Pinus nigra* resistant to *Dothistroma pini* (background) adjacent to a suspectible Spanish source (foreground).

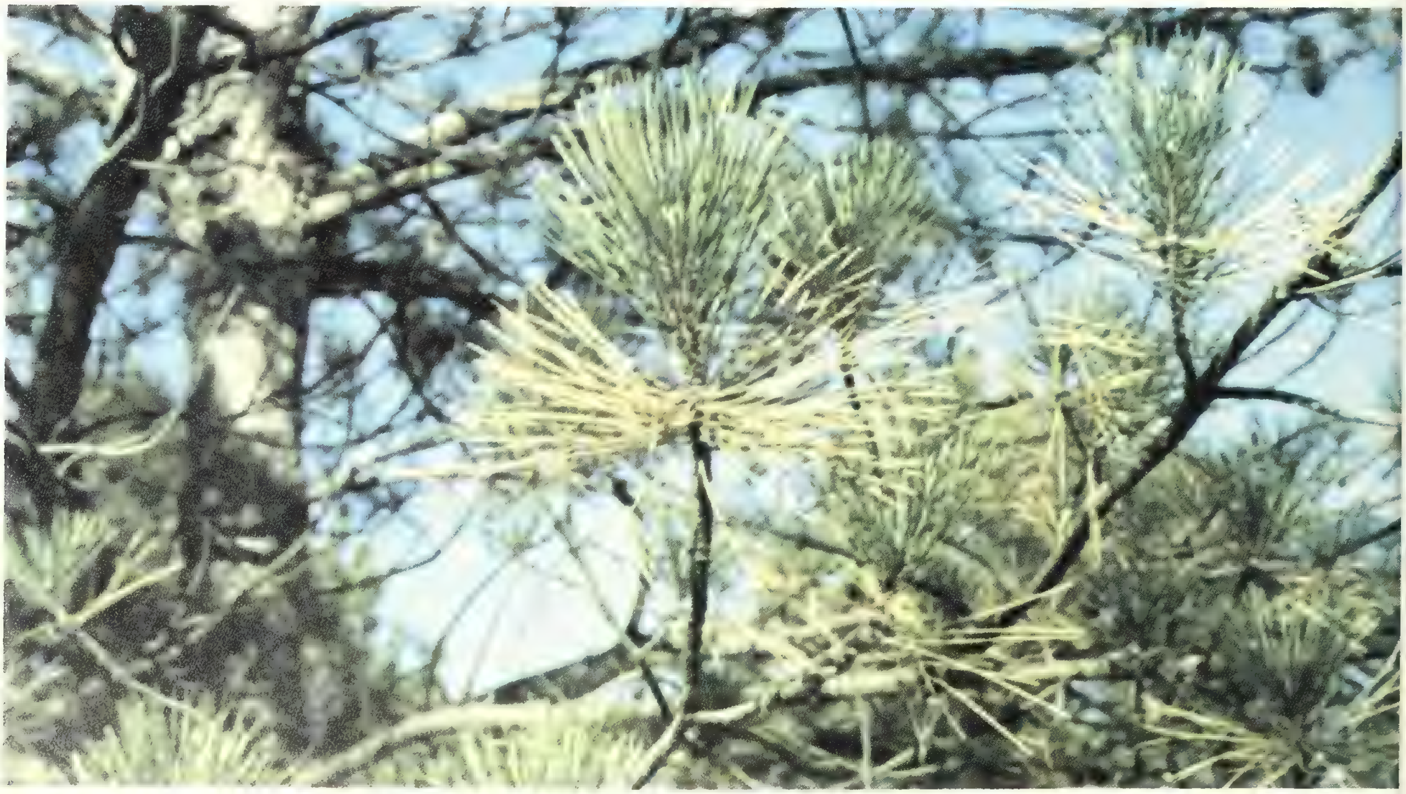


Figure 1-19.—Austrian pine with resistant first-year (current-year) needles and susceptible second-year needles (Photographed in November).

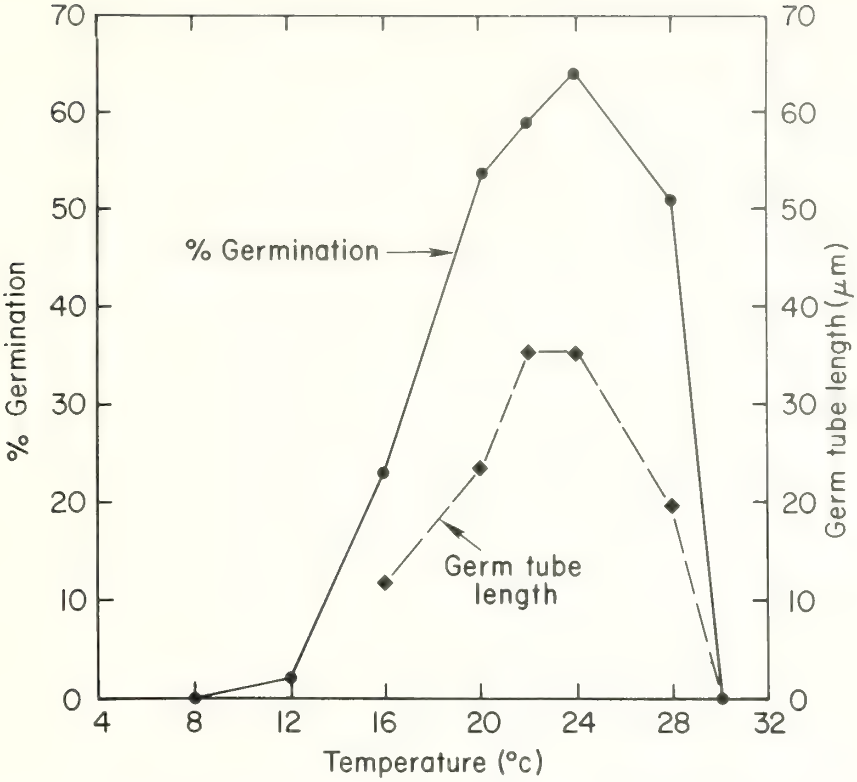


Figure 1-20.—Effect of temperature on germination of *Dothistroma pini* conidia incubated for 24 hours on water agar.

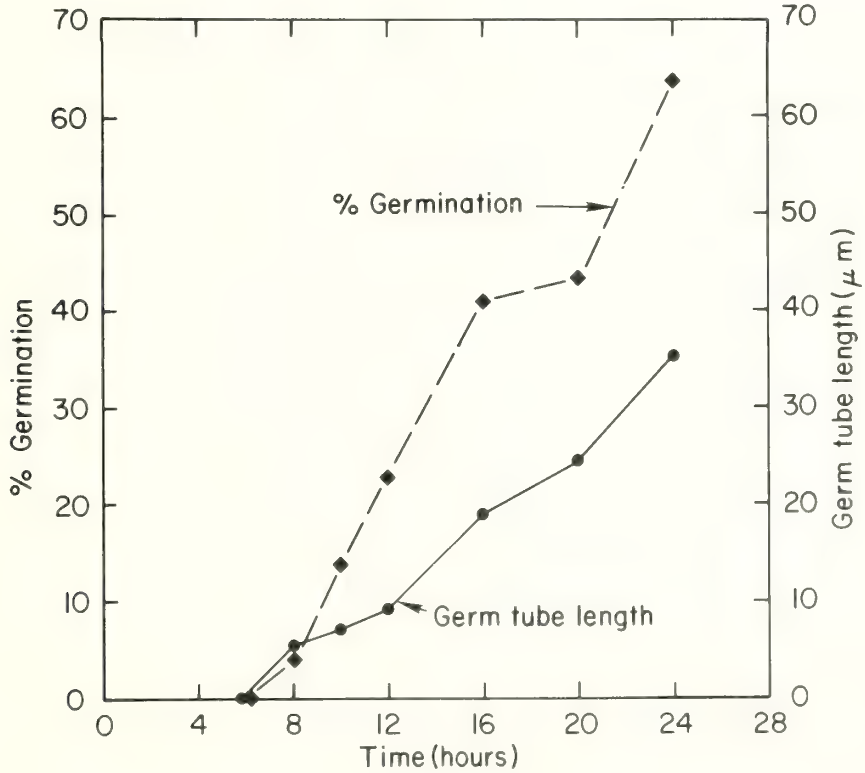


Figure 1-21.—Germ tube length and percent germination of *Dothistroma pini* conidia, incubated for various periods of time, on water agar, at 24°C.

2. Brown Spot Needle Blight of Pines

Brown spot disease caused by the fungus *Scirrhia acicola* has affected pines in the Great Plains, particularly pines in Christmas tree and landscape plantings. Ponderosa and Scots pines have been the hosts most commonly infected in the Great Plains.

The disease caused by this fungus is very similar to the blight caused by *Dothistroma pini*. Infected needles are cast prematurely, and prior to being cast, become discolored (brown). Some of the discolored needles remain on trees for months, thereby destroying the esthetic value of pines in landscapes and making Christmas trees unmarketable.

The most severe damage by the brown spot fungus occurs outside the Great Plains. Large economic losses caused by this fungus occur in plantings of longleaf pine in southern states. Damage to Scots pine in Christmas tree plantings has been more severe in states east of the Great Plains.

Diagnosis

Brownish spots and bands develop in infected Scots and ponderosa pine needles. The tips of the needles become tan, then necrotic, with the bases of the needles remaining green. Later, the bases turn brown. Most diseased needles are cast in the fall, but some are not cast until the following growing season.

Symptoms and damage caused by *S. acicola* are similar to those caused by *D. pini*. *Dothistroma pini* infected needles also develop spots and bands, and the tips of needles become necrotic first, with bases remaining green. Symptoms of brown spot develop earlier than do symptoms of Dothistroma blight. Initial symptoms developed in July, on Scots pine, in a provenance planting, in eastern Nebraska, during the same year, and on the same experimental tract, in which initial symptoms of Dothistroma blight on Austrian pine did not develop until October.

Scots pine, which is highly susceptible to *S. acicola*, is highly resistant to *D. pini*. Ponderosa pine, however, is highly susceptible to both fungi. It is very difficult to distinguish the two blights on ponderosa. Not only are the symptoms similar, but the fruiting bodies are also similar. These two fungi are best distinguished by differences in their spores. Both fungi produce long, cylindrical conidia (spores) which have from 1 to 5 (usually 3) cross walls; however, *S. acicola* conidia are greenish brown, whereas *D. pini* conidia are transparent (hyaline). There are also differences in size of the conidia of the two fungi. A specialist may have to be consulted to make the distinction.

Life Cycle

The primary inoculum is spores which develop in the spring, from fruiting bodies formed after infection the previous growing season. The spores are dispersed principally by rain splash, and are not dispersed long distances. Investigators working in Wisconsin found that generally there are two periods when many spores are dispersed — one in June and one in late August-September (Skilling and Nicholls 1974). They also found that young, growing, Scots pine needles are more susceptible to infection than are mature needles. Therefore, spores released late in the summer apparently cause little infection, because the current-year needles are more resistant than they were earlier in the year. Severe infection occurred between June 26 and July 24, but infection was slight after July 24.

The short-needled varieties of Scots pine, particularly those from France and Spain, are especially susceptible to *S. acicola*. In a planting of 36 geographic sources of Scots pine the short-needled Spanish and French sources were the first to have a significant level of infection.

Scots pine from these geographic sources are growing on an experimental tract which also contains 22 geographic sources of *P. nigra*. The level of infection by *S. acicola*, even in Scots pines from the most susceptible geographic sources, has been much lower than the level of infection by *D. pini* in 21 of the 22 geographic sources of Austrian pine.

However, infection of Scots pines by *S. acicola*, in some Christmas tree plantings, in southeastern Nebraska and in northeastern Kansas, has reached the level requiring control by fungicides. Ponderosa pine also has been heavily infected in southwestern Missouri.

Control

Protective fungicides will control the brown spot needle blight fungus. Several fungicides are effective including Bordeaux mixture and chlorothalonil (Bravo, Daconil),[2] which are EPA registered. In the north-central region, a single application in mid-June is usually sufficient. In severely infected plantations or during unusually wet years, a second spray applied 3 to 4 weeks later may be required.

Where brown spot disease is a serious threat, highly susceptible varieties of Scots pine, such as some of the short-needled Spanish and French varieties, should not be planted.

Physiology and Morphology

Readers are referred to the bulletin by Siggers (1944) and the article by Wolf and Barbour (1941) for information on the physiology and morphology of *S. acicola*.

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[2] *Mention of a trade name or proprietary product does not constitute a guarantee or warranty by the U.S. Department of Agriculture, and does not imply its approval to the exclusion of other products that also may be suitable.*

3. Naemacyclus Needle Cast of Pines

The fungus *Naemacyclus minor* occasionally has caused premature needle cast of pines in the Great Plains. Moderate damage has been found in pines, in Christmas tree plantings, in Kansas, Nebraska, and South Dakota. Hosts in these plantings include Austrian, ponderosa, and Scots pines. This fungus has often been considered a weak parasite; yet, it is currently considered the most damaging pathogen in Scots pine Christmas tree plantings in Pennsylvania. Considerable research has been conducted on the disease by plant pathologists at Pennsylvania State University.

Diagnosis

Diagnosis is relatively easy because of the distinctive fruiting bodies (apothecia) which form on necrotic needles. The fruiting bodies arch upward in a cushion shape, so that the epidermis lying above them splits longitudinally along lines of stomates. The torn epidermal pieces are flapped outwards (fig. 3-1). The torn epidermis pieces can be observed with the unaided eye and can readily be seen with a hand lens. The upper surface of the fruiting body is dull, cream white.

Life Cycle

Investigations of the life cycle of this fungus have been conducted in Pennsylvania but not in the Great Plains. The information on the life cycle presented here has been drawn from the research in Pennsylvania (Kistler and Merrill 1978).

Symptoms develop in September and October after a 10- to 15-month incubation period. The first symptoms are small, light-green spots which develop in September. The spots enlarge and lighten in color; eventually the whole needle becomes yellow with prominent, transverse, brown bands. Symptoms develop first on the second-year needles and on third-year needles not infected the previous year. Foliage of severely infected pines appears distinctly yellow. Most of the infected second-year and third-year needles are cast in October and November, and the characteristic waxy fruiting bodies then form on the cast needles. Some infected necrotic needles remain attached to the tree throughout the winter. These attached needles may bear fruiting bodies, or fruiting bodies may develop on them the following spring. Severely diseased trees retain only the current year's needles.

Ascospores of *N. minor* are released throughout the growing season. The work in Pennsylvania indicates that the principal infection period is July-August. Isolations from needles of different ages have shown that *N. minor* is present in a high percentage of symptomless needles. On many trees, there is no external evidence that the needles have been infected until fruiting bodies develop on them, after they have been normally (not prematurely) cast. In Nebraska, fruiting bodies of *N. minor* have been found on normally cast needles of healthy ponderosa and Scots pines.

An experimental planting in North Dakota, containing many geographic sources of Scots pines, was severely diseased by *N. minor* (fig. 3-2) in the early 1970's. An experiment was established in 1974 to obtain information on when infection occurs and how the disease could be controlled. There had been extensive premature needle casting in the planting in 1973. Most of the second-year needles were necrotic (fig. 3-3). However no new damage occurred in the planting in 1974, nor has there been any significant damage by *N. minor* in the planting since 1974. The reason for the absence of disease in the planting is not known; however, there are several possible explanations. Every other tree (50% of all trees) in the planting was removed in the summer of 1973. The change in moisture conditions resulting from tree removal might have been unfavorable for infection. Also, reduction in moisture stress on trees in the 10-year-old planting might have been involved. Perhaps the weather conditions (rain, temperature) since the epidemic have not been favorable for infection.

Control

The Naemacyclus needle cast fungus can be controlled by protective fungicides. Investigators in Pennsylvania have found two fungicides that are effective. Registration of these fungicides will be sought when their research on timing of fungicide application is completed, probably in 1982. The timing of the first application depends upon conditions which influence the development of fruiting bodies and spores of the fungus. In some years conditions favorable for development occur in early April in Pennsylvania; thus the initial fungicide application should be made by that time. Depending on the year and the fungicide used, control has been obtained with from one to three fungicide applications.

Physiology and Morphology

After an extensive morphological and taxonomical study of *Naemacyclus niveus* and related species, H. Butin suggested that two species of *Naemacyclus* exist on pine needles. The one species, *N. niveus*, was described in the last century; the other species, *N. minor*, was described by Butin in 1973. The *Naemacyclus* species found on ponderosa and Scots pines in the Great Plains is considered to be *N. minor*. The mycelial growth of Great Plains isolates is as described by Butin for *N. minor*, that is thick aerial mycelium develops which later collapses so that the hyphal layer appears dissolved. The centers of colonies are dark brown. Apothecia form in culture.

The following is from Butin's description: asci are cylindrical to club-shaped, 110-115 μm long, 11 μm wide with 8 ascospores; ascospores are hyaline, often twisted, 65-98 μm long, 2.5-3.0 wide, with two septa, paraphyses are filiform, branched at the tip and light yellow. The average length of the 30 ascospores from each of 12 collections in the Great Plains ranged from 70 μm to 89 μm. The length of ascospores of all isolates averaged 80 μm. These data are similar to those reported by Butin.

Pennsylvania investigators report the optimum temperature for mycelial growth *in vitro* as 25°C and for ascospore germination as 22°C.

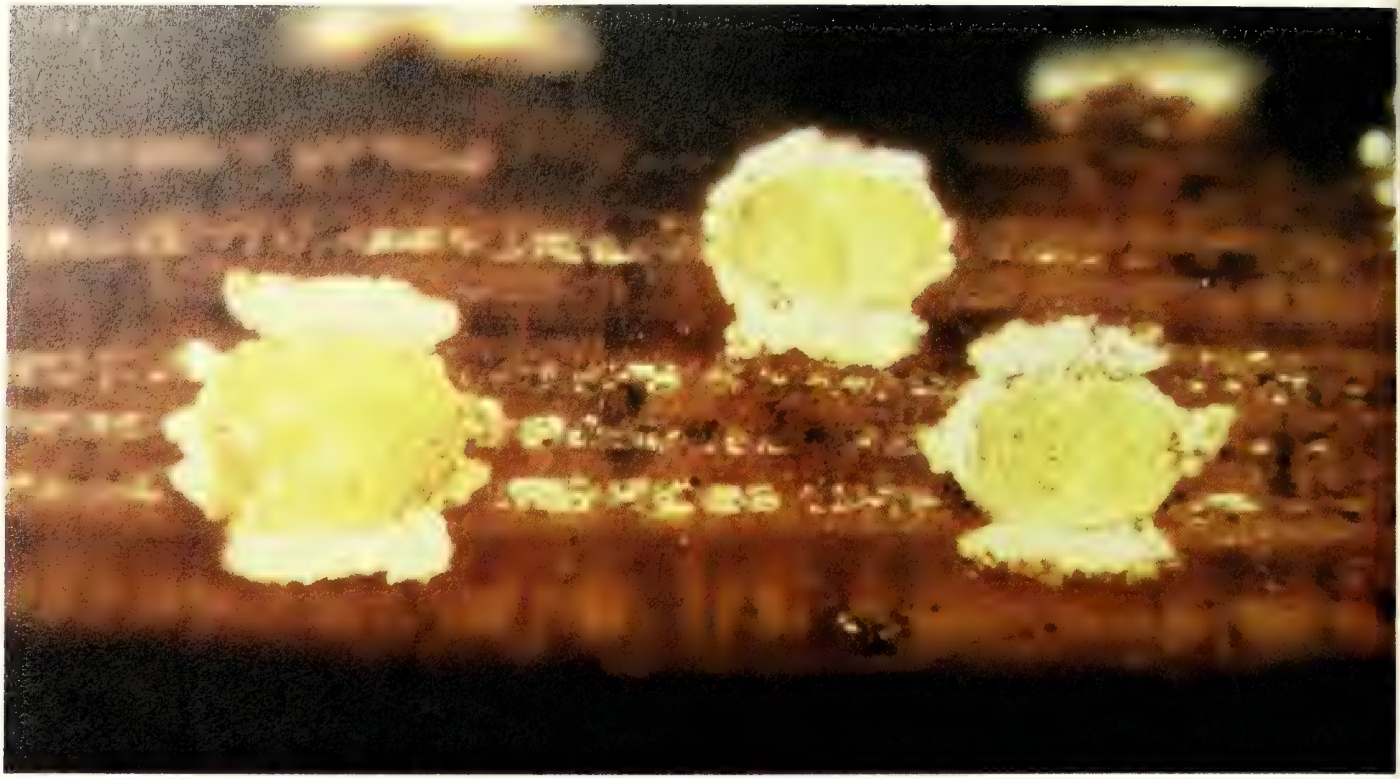

Figure 3-1.—Fruiting bodies of *Naemacyclus minor* on Scots pine needle.

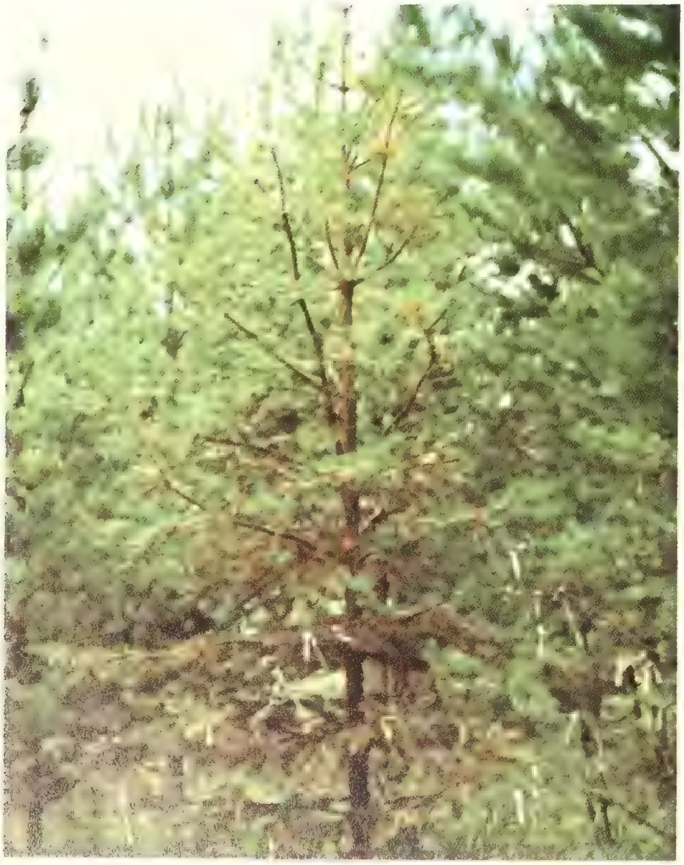

Figure 3-2.—Scots pine infected by the needle cast fungus *Naemacyclus minor.*

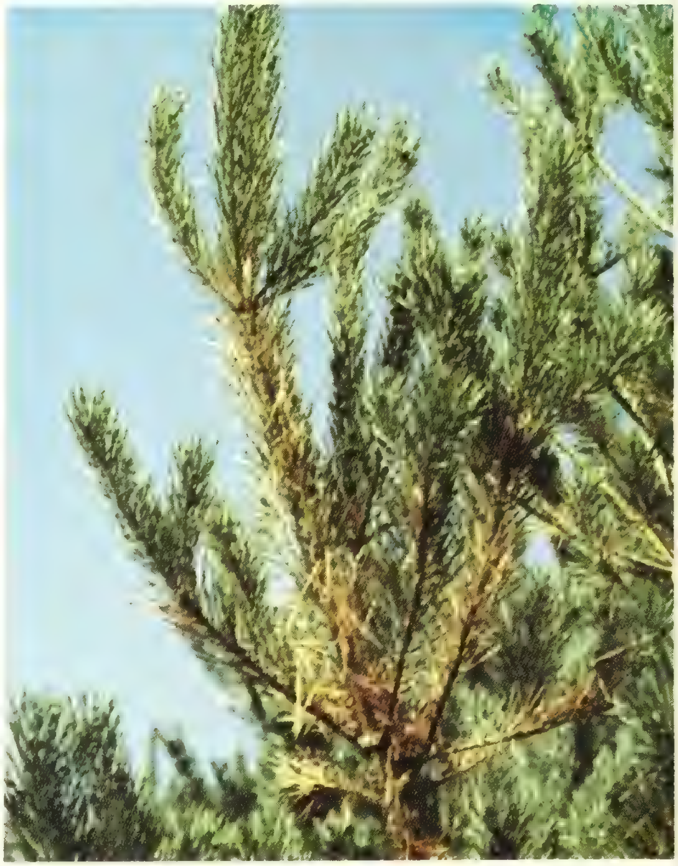

Figure 3-3.—Previous years' needles of Scots pine infected by *Naemacyclus minor.*

4. *Diplodia pinea* Blight of Pines

The fungus causing Diplodia blight infects new shoots of pines. Commonly, the entire new shoot is killed. Older stem tissues also become infected, with the result that major branches are killed back to the main stem. This fungus can destroy the protective value of pines in shelterbelts and windbreaks and the esthetic value of pines in landscapes (fig. 4-1).

Diplodia pinea is widely distributed in the United States (fig. 4-2). Many pine species are infected by this fungus; however, major damage has occurred in plantings of exotics. In the United States, it has been most frequently reported on Austrian pine, which has been widely used in landscape plantings. Other common hosts in the United States are ponderosa, Scots, red, Monterey, and mugo pines. Damage does occur to native species but primarily in plantings; this fungus has seldom been reported in natural pine stands.

Diagnosis

Diagnosis of *Diplodia pinea* blight is relatively easy. Symptoms of the disease are distinctive, and fruiting body location and appearance are such that confusion with other fungi is unlikely.

Droplets of resin usually can be found on infected new shoots before the needles have broken through fascicle sheaths (fig. 4-3). A close examination of such shoots usually reveals that one or a few needles are shorter and darker in color than the rest.

The fungus rapidly invades and kills all needles and tissues of new shoots (fig. 4-4). Commonly, this will occur after the needles have broken through fascicle sheaths but well before needles have reached full size. Early June is a good time to check for new infections.

Because new shoots can be killed by other agents, additional information is needed to determine whether the observed damage is by *D. pinea*. The best field evidence comes from observation of fruiting bodies of the fungus. The dark fruiting bodies (pycnidia) erupt through the epidermis. They usually are numerous at the base of needles and are particularly numerous on the section of the needle covered by the fascicle sheath (fig. 4-5).

The time of appearance of erumpent fruiting bodies on new shoots varies considerably. Fruiting bodies are rarely found on newly infected needles before late summer or early fall. In some years, they are not numerous until the following spring. When symptoms observed in late spring or early summer on trees infected for the first time indicate *D. pinea* infection, pycnidia will not be present on needles. However, this problem can be overcome by placing needles with symptoms in a moist chamber for 48 to 72 hours. If the needles are infected with Diplodia, pycnidia will develop on the needles.

Pycnidial development is not uniform on all needles of a shoot killed by Diplodia. Needles which are ashen gray and which can be detached easily from the shoot should be checked for presence of pycnidia. Needles which are tan or reddish-brown are not suspect.

Whether Diplodia has infected the tree also can be determined by examining second-year or older seed cones. Pycnidia develop profusely on scales of these cones (fig. 4-6). However, pines may have infected second-year seed cones but not infected shoots.

For the specialist with access to microscopes and facilities for culturing fungi, additional identification checks can be made. First, a check can be made to see if the spores are typical of *D. pinea* in size and color (fig. 4-7). Spores of *D. pinea* are colorless (hyaline) when formed but become dark brown. There is a problem when considering another characteristic typical of spores of fungi in the genus *Diplodia*. Spores in the genus *Diplodia* usually are one-septate (two-celled); however, mature dark colored spores of *D. pinea* seldom are one-septate. Spores usually do not have any septations. They do have the potential for forming a septum, however.

Life Cycle

Spores are dispersed beginning before buds start to open and new shoots develop. Thus the fungus is ready to infect the new shoots as soon as they develop. Although shoots can be infected through wounds, infection of new shoots does not depend on wounding.

Diplodia pinea infects not only the tissues (foliage and stem) of new shoots, but infects seed cones as well. The seed cones of ponderosa, Austrian, and Scots pines are not susceptible the year they emerge but are susceptible the second year. Numerous fruiting bodies develop on scales of infected, second-year cones. The pycnidia on cones are an abundant source of inoculum for infection of new shoots. Damage to older pines is attributed to the fungus first infecting second-year seed cones, then spores from pycnidia on the seed cones infecting new shoots. Several years' observations have revealed that second-year seed cones may be infected before new shoots are significantly infected.

In the central Great Plains, damage usually does not become severe until after pines are 30 years old. Pines in plantings less than 30 years old have been damaged, but usually when younger plantings were established near older pines.

Infected seedlings in nurseries usually are in beds which have been established near older, cone-bearing pines. Container-grown pine seedlings placed in the shade of Diplodia-infected pines to harden-off have been destroyed by *D. pinea*.

Several years after shoots are first infected, *D. pinea* damage occurs to older stem tissues. This damage may extend the length of major branches, killing them back to the main stem (fig. 4-8). Occasionally there is extensive killing of branches at the top of trees (fig. 4-9). Commonly, all tissues of infected first-year shoots are killed back to the node. Although it reasonably might be expected that the fungus grows from the infected new shoots into adjacent and older internodes, periodic observations of branches containing infected new shoots did not reveal a single case in which the adjacent older tissues became infected. Histological studies of stem tissues at the node between current-year growth and second-year growth, revealed that the fungus present in current-year growth did not grow into the second-year growth. *Diplodia pinea* can be readily isolated from older, damaged tissues. Wounds, such as those caused by hail, can become infected; thus wounds would make the older tissues vulnerable to infection. However, examination of infected older tissues has not revealed any obvious wounds, such as those caused by hail. Possibly there are obscure wounds, such as those made by some insects, which could be the infection courts.

Because seed cones become infected the second year, possibly the fungus grows into the second-year and older stem tissues via the peduncle of the cones. The fungus has been consistently isolated from the scales, axis, and peduncle of cones; however, the fungus has not been isolated from stem tissues subtending infected peduncles of cones.

When infected new shoots die, buds are frequently forced just beneath the dead shoot. A check of shoots developing from the forced buds has not revealed that they are an avenue by which the fungus enters older stem tissues.

Thus the avenue of infection of older stem tissues which are free of gross wounds is not known. Specific-aged internodes were inoculated to determine if the fungus will grow across proximal and distal nodes and damage adjacent internodes. The fungus did not grow into adjacent internodes.

Control

Infection of new shoots can be reduced effectively by properly timed applications of fungicide. The following information on infection and disease development has been useful in determining when fungicides should be sprayed (fig. 4-10).

Generally, the temperatures prevailing during the early period of shoot formation are favorable for spore germination and germ tube growth. Through field inoculations, made at different times, of newly developing shoots of Austrian, ponderosa, and Scots pines, infection was found to occur as soon as buds begin to open. Infection continued to occur until approximately mid-June. A series of tests extending over 3 years was made to determine when, during the period from bud opening (approximately April 24 in eastern Nebraska) to mid-June, the shoots were most susceptible. The period of susceptibility was found to be a 2-week period beginning with bud opening (fig. 4-10). This period in eastern Nebraska is approximately April 24 to May 8. Applying fungicide after May 15 was of no value.

Because cones are an abundant source of inoculum, removal of infected branches (sanitation) does not have a significant effect on infection intensity. Spores are produced on leaf and stem tissues, but the numbers produced are small in relation to the numbers produced on seed cones.

Fungicide applied to control shoot infection has not been effective in preventing infection of second-year cones. This is not surprising, because the seed cones still are rapidly expanding after the period (April 24 - May 8) in which fungicide is applied for control of shoot infection. Thus the surface of expanding cones is not adequately covered by the early fungicide applications.

Physiology and Morphology

Diplodia pinea grows rapidly on potato dextrose agar and other commonly used media. Colony growth was optimum at 28°C (fig. 4-11). A high percentage of conidia of *D. pinea* germinated in the temperature range 16°C to 36°C (fig. 4-12). Germ tube growth was greatest at 28°C. A high percentage of conidia germinated within 2 hours, and germ tube growth was very rapid after 2 hours (fig. 4-13).

Pycnidia develop when *D. pinea* is cultured on media such as potato dextrose agar; however cultures need to be incubated in the light. After 10 days, incubation at 28°C, under 15-watt fluorescent light, cultures contained 30 pycnidia per cm^2; viable spores were present in one-third of these pycnidia after 10 days.

Isolates vary in their capacity to produce pycnidia. Pycnidial production is often enhanced by growing the fungus on culture media to which sterile pine needles have been added.

The dimensions of D. pinea conidia are in the range 35-40 μm by 16-18 μm.

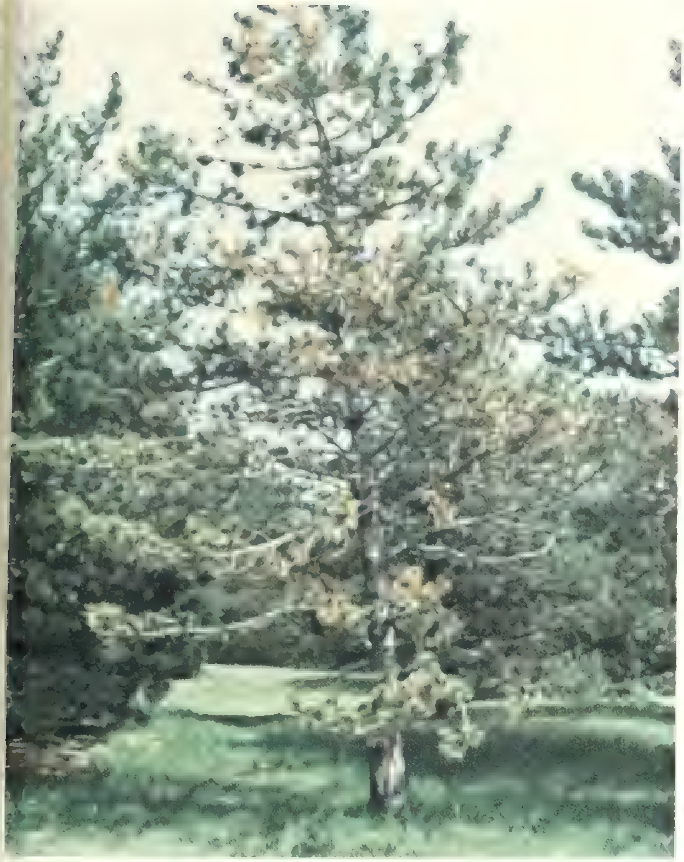

Figure 4-1.—Austrian pine tree infected with *Diplodia pinea.*

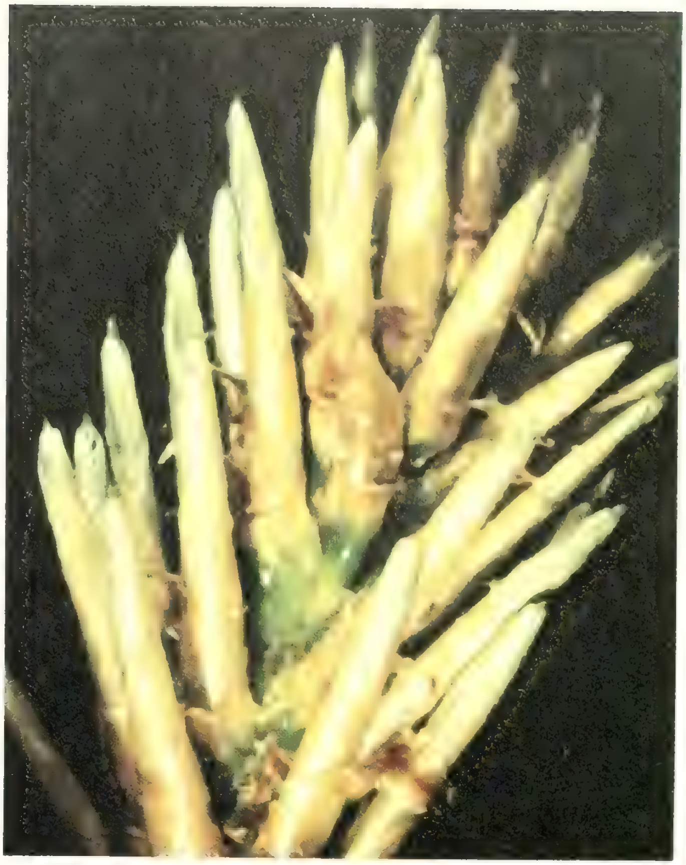

Figure 4-3.—Stunted needle with resin droplet resulting from initial infection of a new shoot by *Diplodia pinea.*

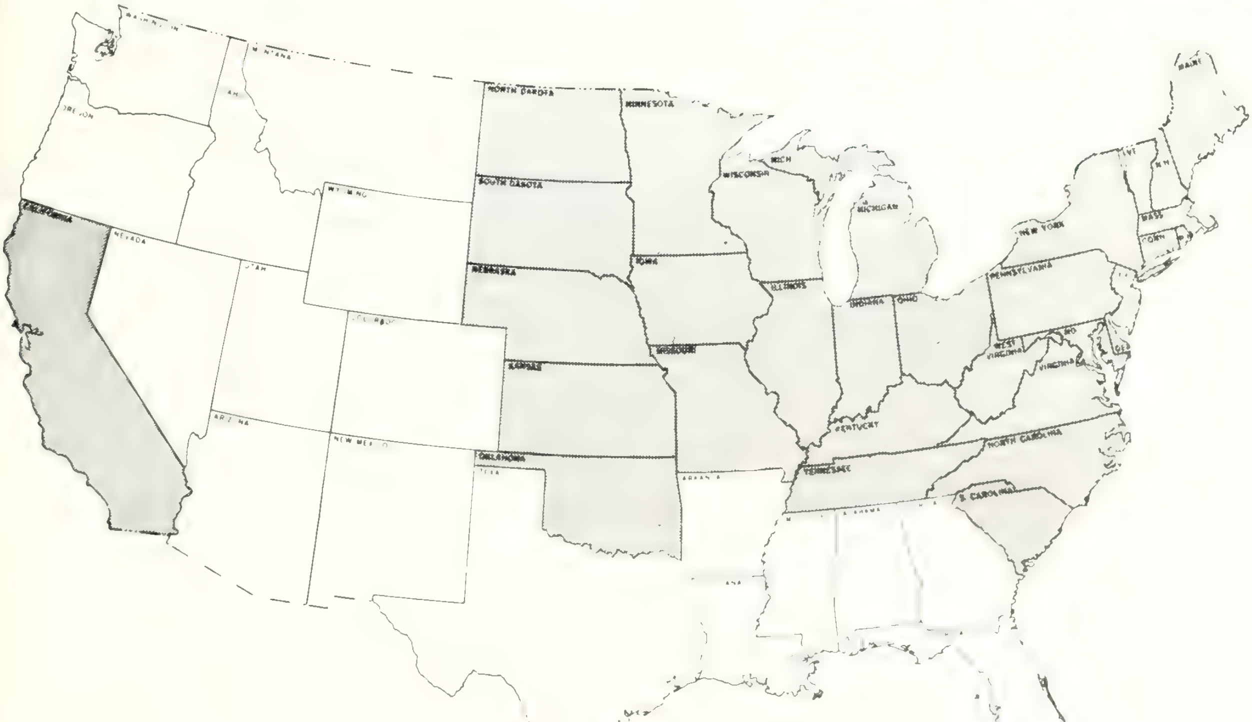

Figure 4-2.—*Diplodia pinea* occurs in shaded states and in Hawaii.

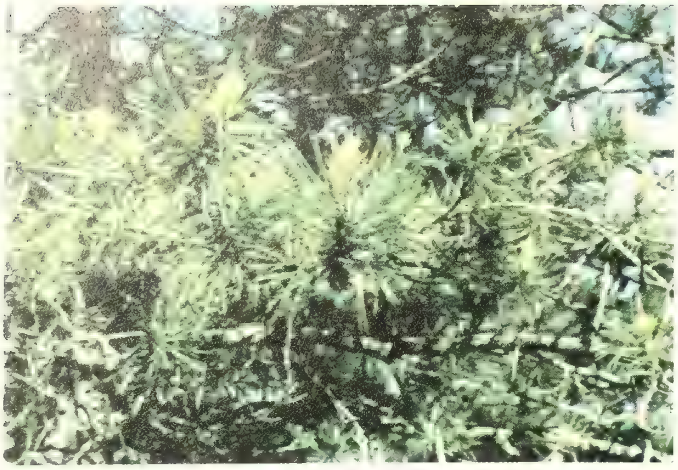

Figure 4-4.—New shoots of Austrian pine killed by *Diplodia pinea.*

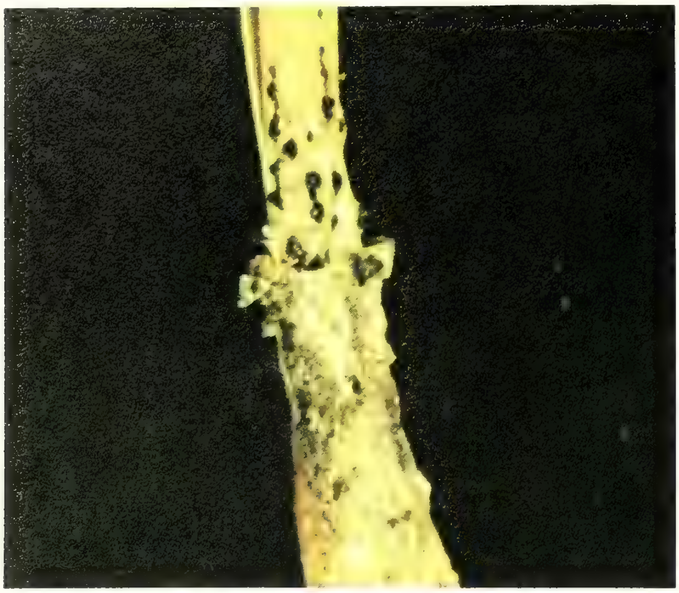

Figure 4-5.—Fruiting bodies (pycnidia) of *Diplodia pinea* numerous at base of Austrian pine needle.

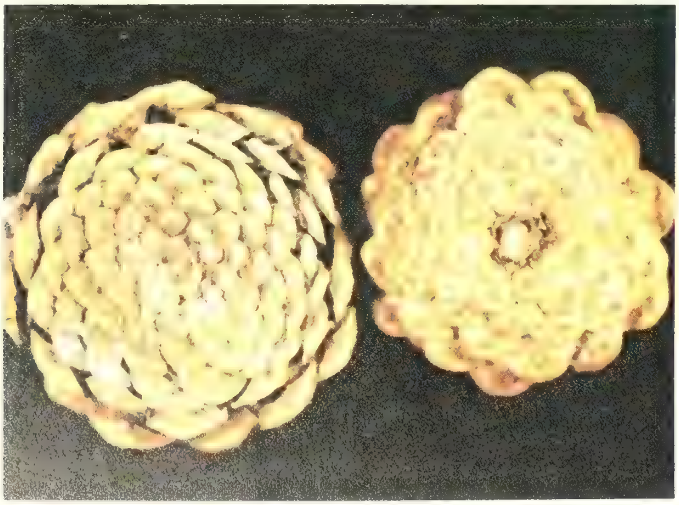

Figure 4-6.—Fruiting bodies (pycnidia) on an Austrian pine seed cone infected by *Diplodia pinea* (left); uninfected cone (right).

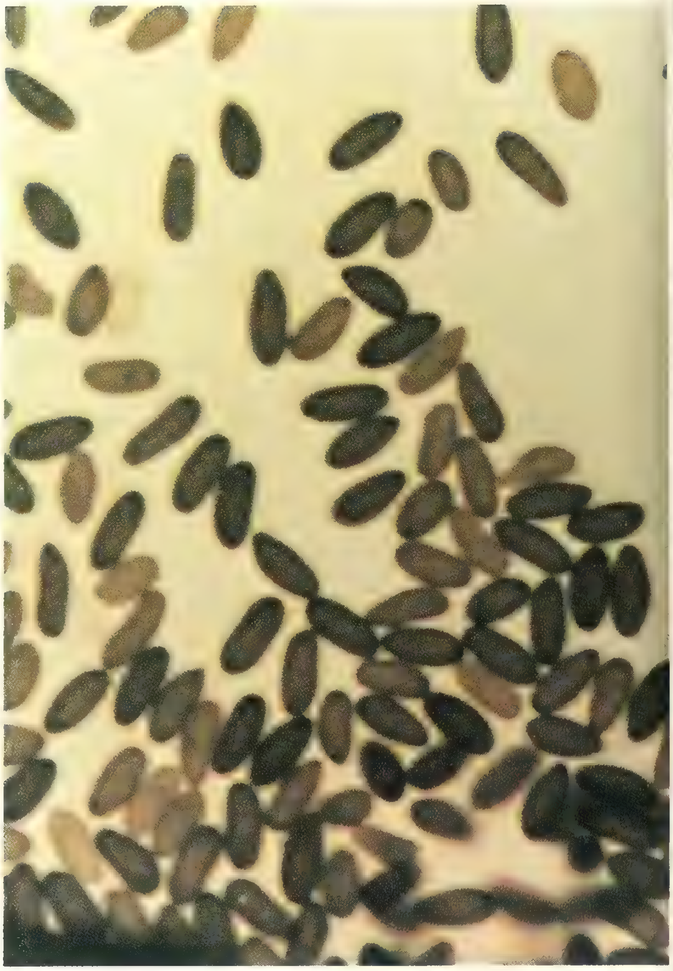

Figure 4-7.—Spores of *Diplodia pinea.*

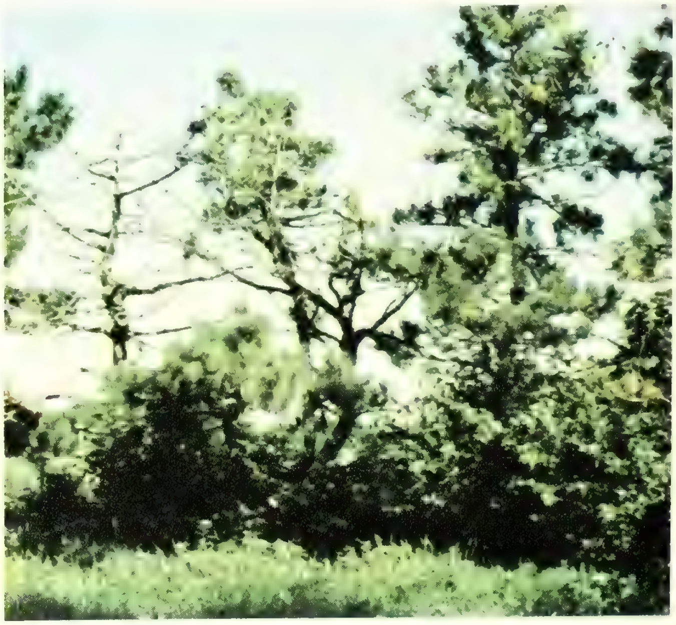

Figure 4-8.—Severe damage to Austrian pines caused by *Diplodia pinea.*

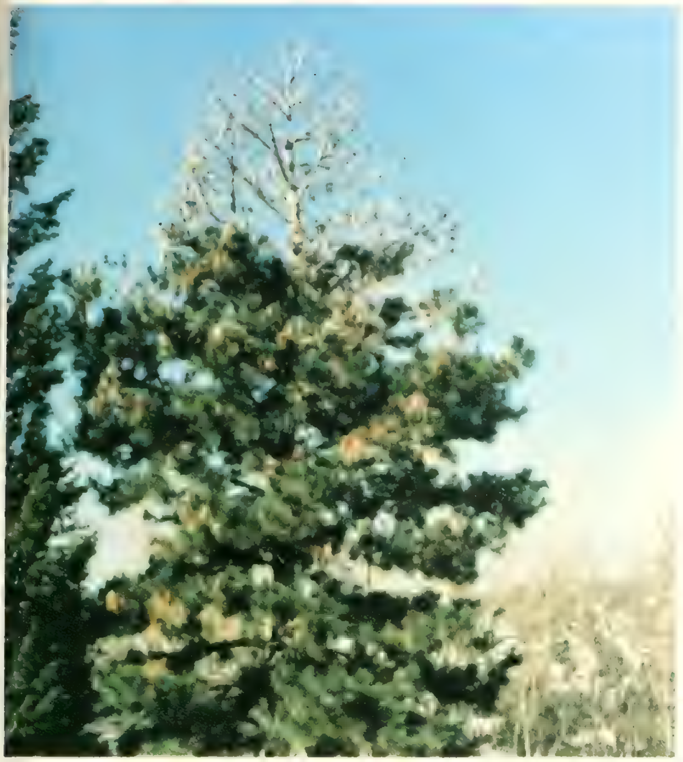

Figure 4-9.—Top of Austrian pine tree killed by *Diplodia pinea*.

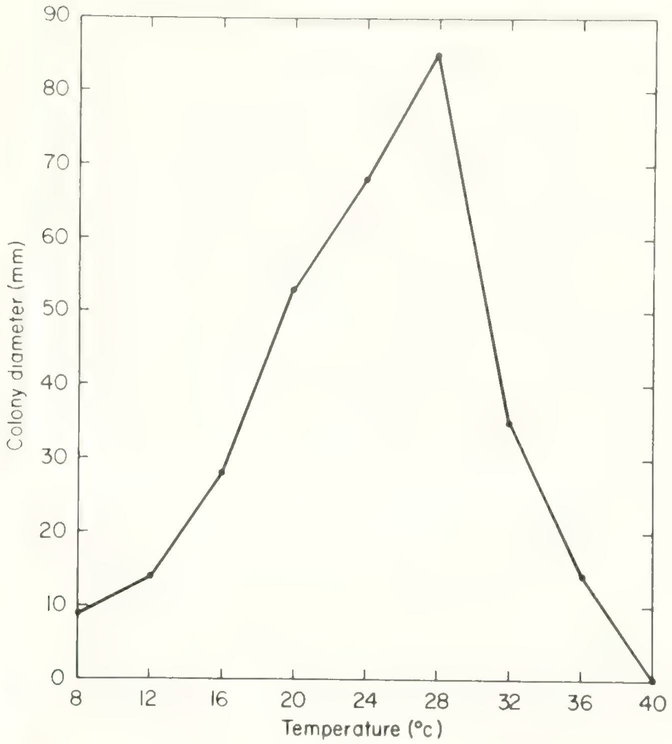

Figure 4-11.—Effect of temperature on colony diameter of *Diplodia pinea* grown on potatoe dextrose agar for 48 hours.

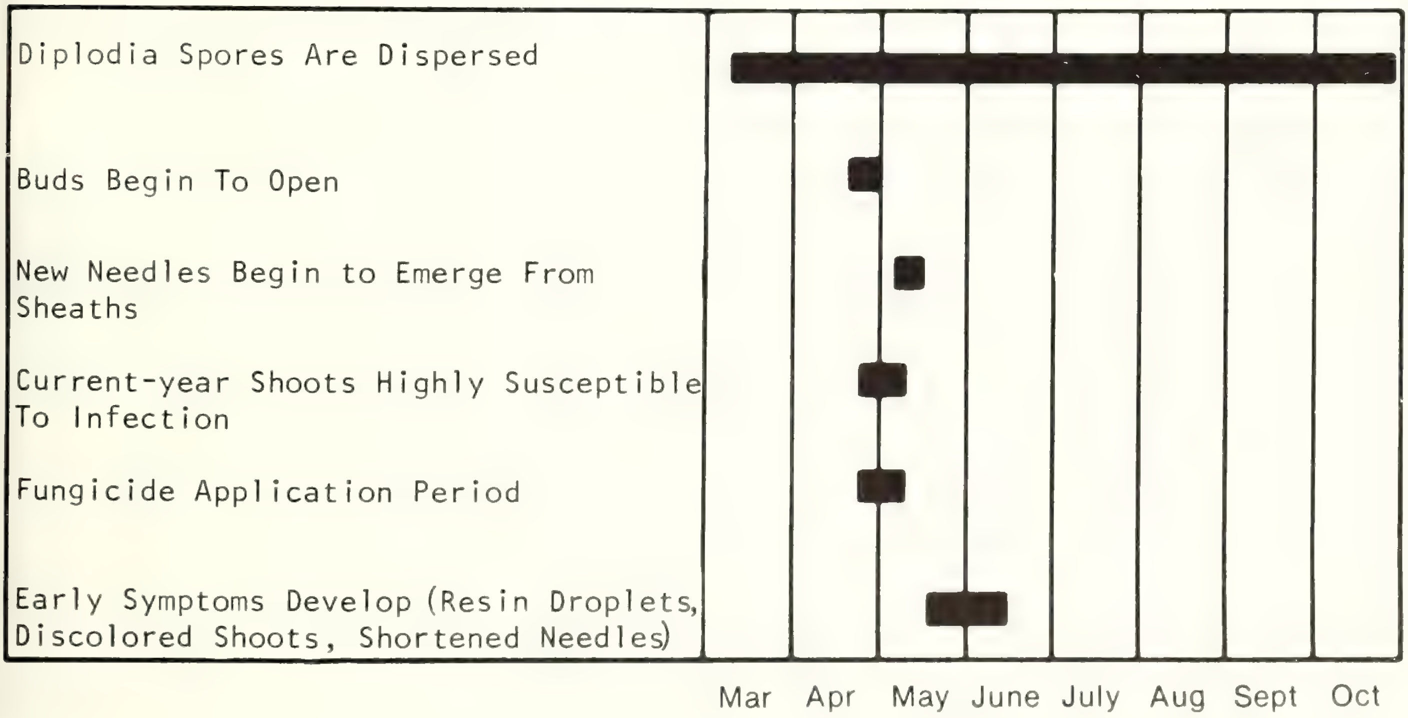

Figure 4-10.—Schedule for developing programs for control of Diplodia blight.

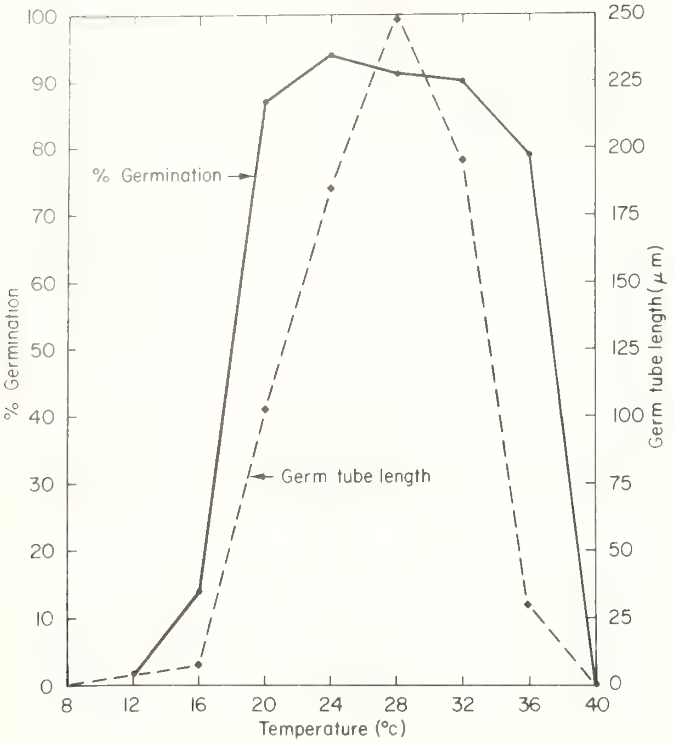

Figure 4-12.—Effect of temperature on germination of *Diplodia pinea* spores incubated for 4 hours on water agar.

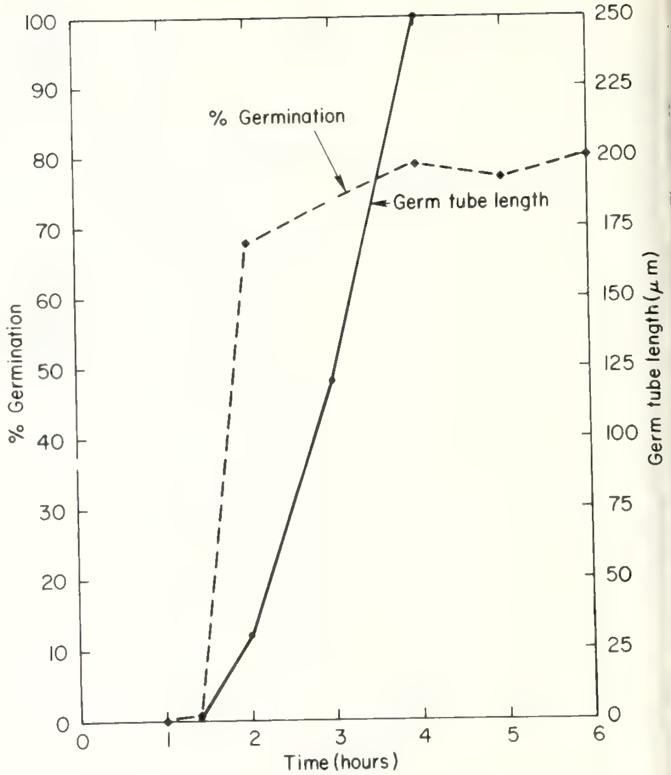

Figure 4-13.—Germ tube length and percent germination of *Diplodia pinea* spores incubated for various periods of time, at 26°C, on water agar.

5. Western Gall Rust of Pines

Infection of pines by the western gall rust fungus *Peridermium harknessii* results in formation of branch and stem galls (figs. 5-1, 5-2) and sometimes cankers. The quality of wood in gall-bearing stems is reduced, and the stems are subject to wind breakage.

Ponderosa and Scots pines are most frequently damaged by this fungus in the Great Plains; however, the fungus has a wide host range, including lodgepole, jack, and mugo pines.

Surveys of all natural ponderosa pine stands in Nebraska, in the early 1920's, revealed that gall rust was present in all the stands. There is a high percentage of infected trees, in natural ponderosa stands, in the Pine Ridge area, in northwestern Nebraska, and in natural stands and plantings of ponderosa in the Black Hills of South Dakota.

Gall rust has seldom been detected in shelterbelts established in the Great Plains. The exception to this is in North Dakota, where plant pathologists at North Dakota State University have found gall rust in a high percentage of shelterbelts.

Diagnosis

The distinctive galls which develop on infected trees make it easy to detect western gall rust (fig. 5-3). This rust can be confused with eastern gall rust (*Cronartium quercuum*) because the galls of both are similar. The two fungi can be distinguished by differences in germ tubes developing from spores formed in galls. Determining these differences requires germination of the spores and comparison of growth rate and branching of germ tubes, a task best handled by specialists.

Life Cycle

The galls on pines produce spores in the spring. These spores are dispersed primarily by wind. The main period of spore dispersal is in May and early June. The spores infect newly developing shoots of pines. Thus this is a pine to pine rust; that is, infection of pines does not require a non-pine (alternate) host. In contrast, eastern gall rust is a pine-oak rust; spores produced in galls on pines infect oak leaves. The spores produced on the oaks infect pines.

Galls seldom are formed the year trees are infected. Most are formed the second year. They are first evident in July or August. The galls formed in July and August of the second year produce spores the following spring. The surface of the galls breaks open, exposing the bright-colored spores (fig. 5-4, 5-5). The spores are wind-dispersed in May and June.

The time between initial infection and sporulation is approximately 24 months. In rare instances, galls form on shoots during the same growing season that the shoots are infected; these galls then produce spores the following spring.

Galls continue to produce spores each year. They cease only when the stem tissue bearing galls dies.

The best time to check for infection is in August or later, when galls resulting from infection the previous year are evident. However, if a planting is being checked for the purpose of reducing the amount of inoculum (spores) of the rust fungus, the checks should be made before spores are dispersed in the spring. In most areas, this would mean making the checks before the last week in April. Checks for presence of rust could be made in early summer, but they would reveal only old galls that have already sporulated.

Infection of Nursery Seedlings

Because the spores are dispersed by wind, pines far from a source of spores (infected tree) may become infected. Pine seedlings in nursery beds, located 200 m from old infected pines, became infected. The level of infection was low (less than 0.5%) in the seedling beds. This nursery has routinely checked for presence of rust in pines near the nursery; infected trees or the branches bearing galls are removed.

Infection of nursery stock, even a low percentage of stock, is serious because spores will develop on and be dispersed to other trees in outplantings. Although nurseries certainly do not distribute seedlings which have galls, some infected seedlings will not have galls on them when they are distributed for planting. Seedlings which are infected the last year they are in the nursery will not have galls on them when they are distributed for spring planting. Galls will develop on such seedlings during July and August of the first year they are planted. Typically these seedlings will have galls at the base of the main stem (fig. 5-6).

Rate of Spread in Outplantings

Gall rust was detected in several experimental plantings, established in 1968, which contained from 50 to 80 geographic sources of ponderosa pine. The initial source of infection was obviously nursery stock, because the trees had galls at the base of main stems, and there were no infected pines near the planting sites.

It was determined that approximately 1 seedling in 1,000 was infected in the nursery. Next, the rate of disease spread within the plantings was determined. During annual examinations through the spring of 1977, determinations were made of the number of trees infected and their distance and direction from epicenters (trees initially infected in the nursery). A total of 879 trees were infected; by 1977, 58% and 76% of these were within 26 m and 38 m, respectively, of trees that had been infected in the nursery.

Infected trees were uniformly distributed around epicenters; incidence of infected trees was as high in one direction from the epicenter as incidence in other directions.

There was a high level of new infections in 1973 but not in 1972 or 1974. Some 53% of all diseased trees were initially infected in 1973, and 56% of the total number of galls were on 1973 internodes. Since spores were available for infection during the three years, the yearly variation in infection was probably due to weather conditions (moisture, temperature) being more favorable for infection in 1973.

Control

The level of rust infection was reduced from 4% to less than 0.5% by removing branches containing galls or entire infected trees located near the nursery. This sanitation procedure is carried out each year before galls sporulate in the spring.

During the course of a study on spread of the rust fungus within young, experimental pine plantings, all galls observed were removed. The approximate number of trees in two of the plantings was 5,000 and 8,000. Removing galls no doubt reduced the level of infection; however it was impossible to find every gall no matter how carefully trees were checked. In a planting of 3,000 pines, one tree was found that had been initially infected in the nursery. This tree was removed and a careful check of all trees in the planting was made for 3 successive years. The considerable increase in the number of infected trees in the planting indicates that not all of the galls were found. Perhaps in a very small planting, rust, if detected early, could be eradicated by gall removal.

The best way to ensure that gall rust does not develop in Great Plains plantings is to use nursery stock grown where infection does not occur, that is stock grown where there are no infected pines near the nursery. There are no fungicides that currently are EPA registered for control of this rust fungus in the Great Plains.

Physiology and Morphology

Readers are referred to the bulletin by R. S. Peterson (1967) for information on the physiology and morphology of *P. harknessii*.

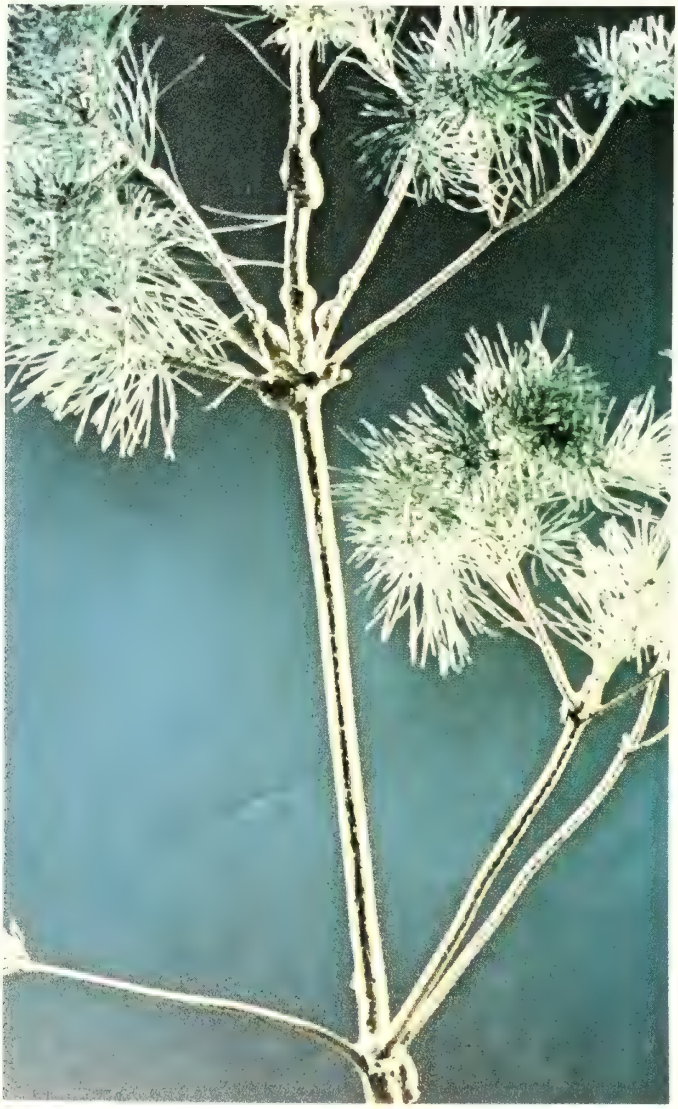

Figure 5-1.—Galls on Scots pine infected by *Peridermium harknessii.*

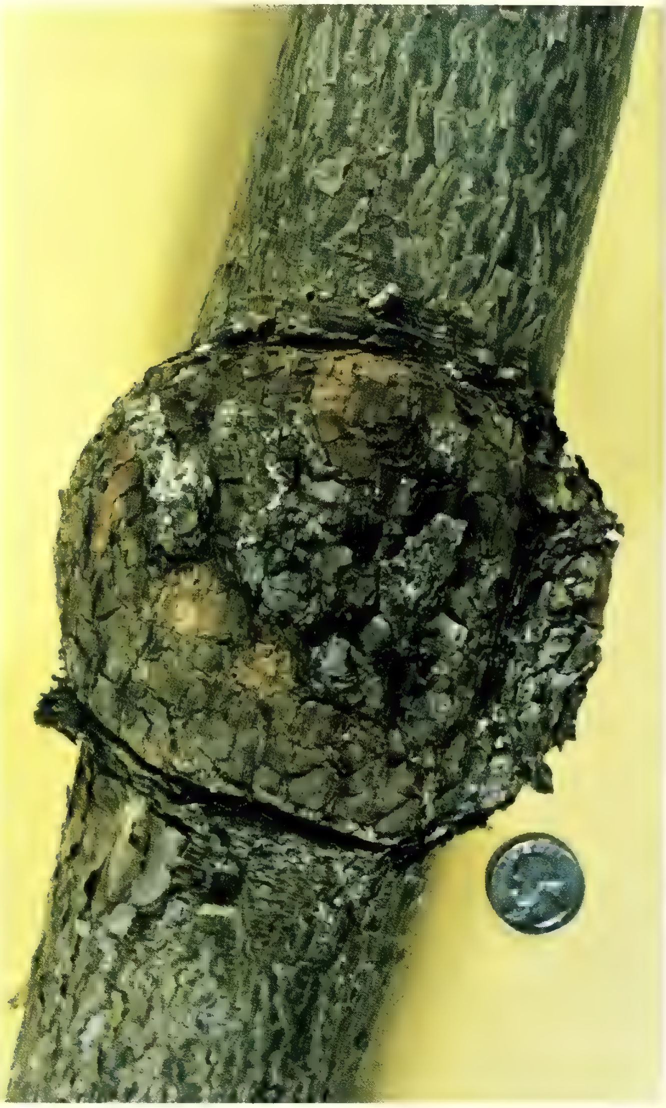

Figure 5-2.—Large gall on stem of Scots pine.

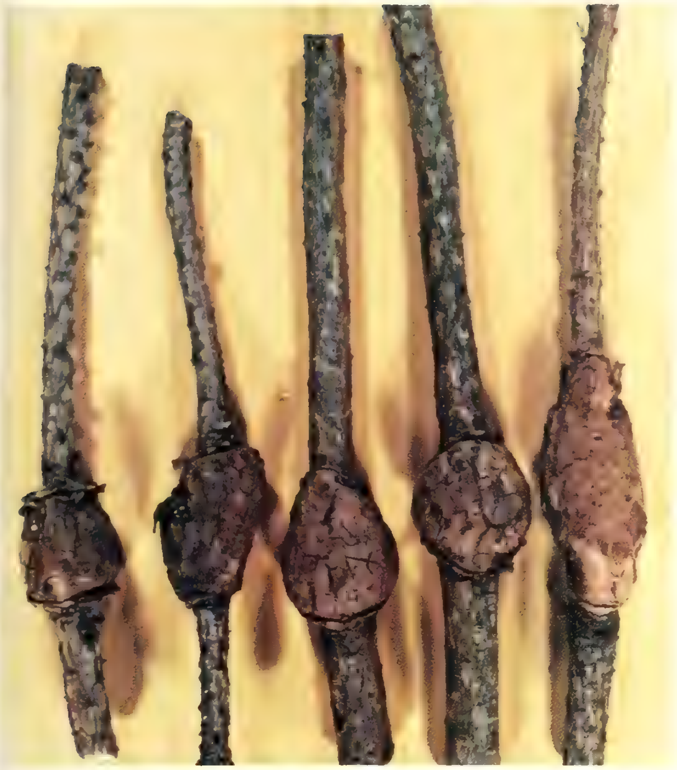

Figure 5-3.—Galls of various shapes on ponderosa pine branches infected by the western gall rust fungus.

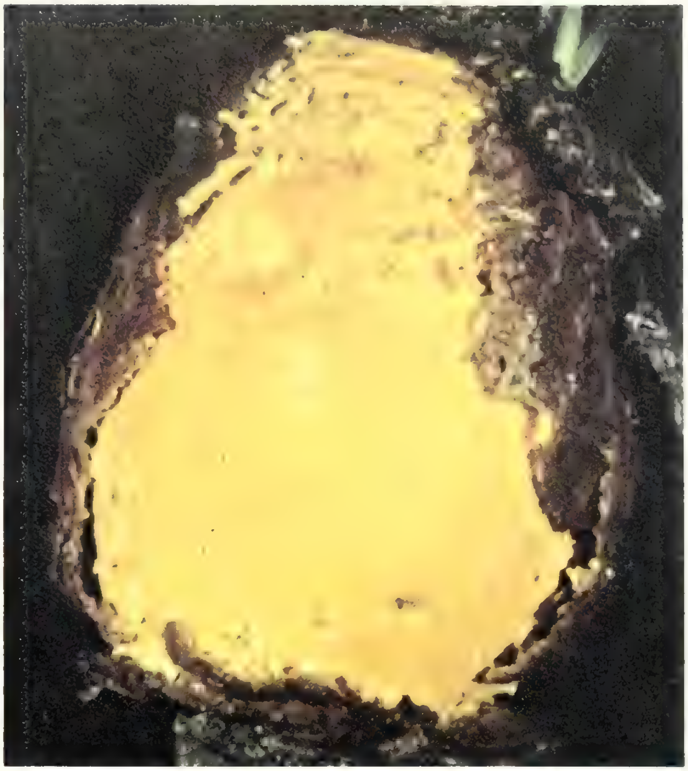

Figure 5-5.—Gall with surface removed, exposing masses of *Peridermium harknessii* spores.

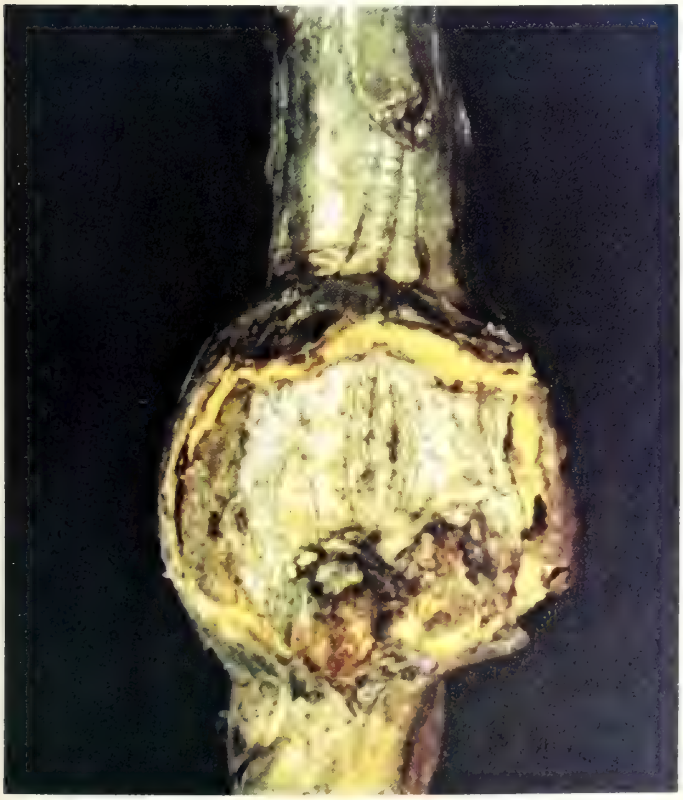

Figure 5-4.—Surface of gall splitting open in mid-May revealing orange spores of *Peridermium harknessii.*

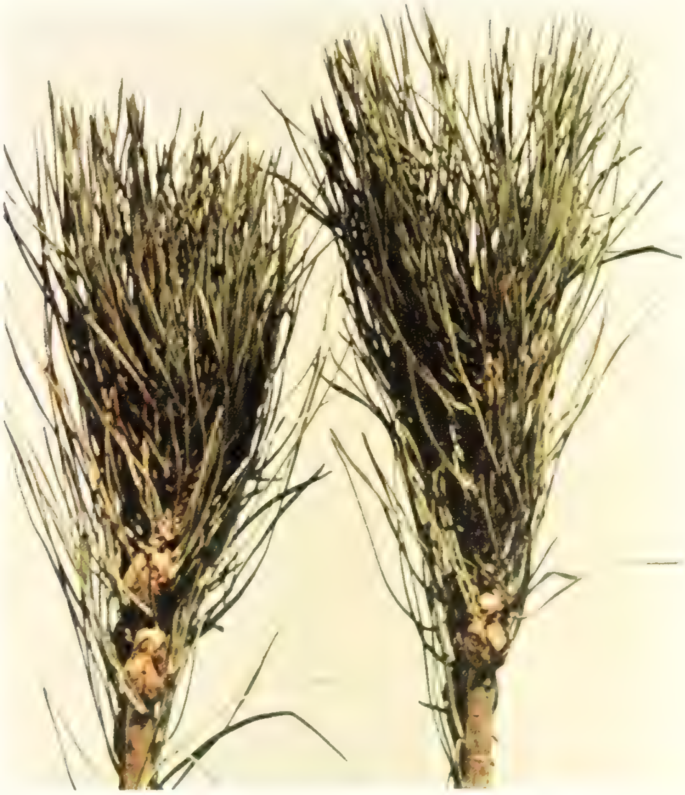

Figure 5-6.—Galls on lodgepole pine seedlings infected in the nursery with *Peridermium harknessii.*

6. Phomopsis Blight of Junipers

Phomopsis juniperovora has been a threat to nurserymen producing junipers since the 1880's (fig. 6-1). This fungus disease is common in the Great Plains, from South Dakota to Texas and eastward to the Atlantic Coast (fig. 6-2). Losses have been especially severe in seedling beds of *Juniperus virginiana* and *J. scopulorum* and in the production of grafted selections of these and other juniper species. *Cupressus arizonica* seedlings have been seriously damaged by this fungus in some southern states. Several other species in the Cupressaceae family are susceptible.

Diagnosis and Life Cycle

Phomopsis initially infects foliage, then spreads to and kills stem tissues. Newly developing needles are especially susceptible while they are still in the yellowish green stage; after needles develop to a normal, deep green, they are not susceptible. Small, yellowish spots appear on needles of *J. virginiana* and *J. scopulorum* within 3 to 5 days after infection. The fungus permeates young needles and rapidly invades young stem tissues (fig. 6-3). As a result, terminals and branches become light green, then red-brown and, finally, ashen gray. When a side shoot is infected, the fungus progresses to the main stem, which it may girdle if the stem is less than 1 cm in diameter (fig. 6-4). The portion of the seedling above the girdled area then dies. Lesions on larger stems frequently develop into cankers, but the stems are not girdled. The fungus does not spread far below cankers. Survival is poor if infected bareroot stock is outplanted. A comparison of blighted and non-blighted trees outplanted in eastern Nebraska revealed that survival of blighted stock after 2 years was 30% less than non-blighted stock.

Phomopsis fruiting bodies (pycnidia), with viable spores, may develop within 3 to 4 weeks after seedlings become infected. Well developed pycnidia are usually found on needles and stems that have dried and turned ashen gray. The small, dark pycnidia are at first embedded in needles and stems, but later they erupt through the epidermis (fig. 6-5). The spores are extruded in whitish yellow tendrils. Two types of spores (alpha and beta) develop in the same or different pycnidia (figs. 6-6, 6-7). Alpha spores are colorless, one-celled, ellipsoid, contain two oil globules, and commonly are 7.5-10 by 2.2-2.8 μm. Beta spores are colorless, one-celled, filamentous, slightly curved, and 20.2-26.9 by 1 μm.

Frequently, only alpha spores are found in pycnidia. This makes disease identification difficult, because there are some saprophytic fungi found on junipers that produce spores similar to Phomopsis alpha spores. However, these spores usually do not have the two characteristic oil globules. Specialists can readily distinguish these saprophytes from Phomopsis by using such cultural media as potato dextrose agar or malt extract agar. On these cultural media, *P. juniperovora* produces a characteristic deep yellow coloration, usually accompanied by appearance of orange-red crystals (Fig. 6-8).

Another fungus, *Cercospora sequoiae*, which causes a blight of junipers and other species in the Cupressaceae family, can be easily distinguished from Phomopsis blight. Cercospora infection originates on older needles of lower branches and spreads upward and outward, whereas Phomopsis infection starts on new needles on branch tips and advances inward.

Damage from drought can be confused with Phomopsis blight. In both cases, tips of branches may be killed. However, the demarcation between green and dead tissue will be sharp in Phomopsis-blighted seedlings but gradual in seedlings affected by drought.

Damage from the lesser cornstalk borer can be distinguished from Phomopsis blight by the straw color of the dead tops and by the feeding wounds on the lower stem and taproot.

Recently, *Kabatina juniperi* has become a problem in juniper outplantings and in production of grafted junipers. This fungus causes symptoms similar to those caused by Phomopsis. However, there are differences in spore size and fruiting bodies between this fungus and Phomopsis, which a specialist can recognize.

Control

Fungicides are needed for effective control in seedling beds (fig. 6-9). Mercury fungicides have been effective against Phomopsis; however, there are now restrictions against use of mercury fungicides. Most of the non-mercury fungicides in general use are not effective against Phomopsis. Bordeaux mixture is frequently recommended for control, but is ineffective. Several relatively new fungicides have been tested in recent years in a South Dakota nursery. The tests have shown that benomyl, which is EPA registered for use against Phomopsis, is effective.

Protective fungicides, such as benomyl, must be applied regularly to protect new growth. In Great Plains nurseries, fungicide is typically applied weekly, beginning with seedling emergence and ending after the last flush of growth in the fall. Because the fungus initially infects only foliage at the yellowish-green stage, infection is highest during periods of new growth. In most Great Plains nurseries, juniper seedlings have a flush of growth in the spring and another flush in late summer or early fall. Some of the worst losses occur during late flushes of growth. In some Great Plains nurseries, there is a period in midsummer when little or no infection occurs, because there is little or no new growth. The frequency of fungicide applications possibly could be reduced during this period. However, more tests are necessary, because 3-0 *J. virginiana*, grown under irrigation in a South Dakota nursery, were infected throughout the growing season whenever branches bearing Phomopsis pycnidia were placed into the nursery beds.

Moderate temperatures (16° to 26°C) and rain are conducive to infection. However, applying fungicides only after rain is impractical, because Phomopsis spores need only about 7 hours to germinate, enter, and infect seedlings. This period would be too short in many cases to prepare equipment and apply spray in time to prevent infection. In addition, tests in South Dakota have shown that, if benomyl is applied weekly at 0.5 pound per acre, residue on new growth is sufficient to prevent disease development, even after periods of moderate rainfall (12 to 22 mm).

Removing infected seedlings from beds (roguing) can reduce the amount of infection, because the disease apparently progresses slowly from infected to uninfected areas of nursery beds, if only a few infected trees are present.

In South Dakota, infected branches bearing Phomopsis pycnidia were placed into uninfected 2-0 *J. virginiana* beds when new growth began in the spring. One month later, all new infection was within 1 foot of the branches that had been placed into the beds. Infected seedlings should be rogued only when they are dry, to minimize the spread of spores. Rogued seelings should be immediately placed in a container, such as a plastic bag, to minimize chances of spores being dispersed. The infected seedlings then should be disposed of carefully. Weekly roguing of all seedlings with dying foliage, coupled with benomyl sprays at 7- to 10-day intervals, has provided complete control of Phomopsis blight at the Big Sioux State Conifer Nursery, Watertown, S. Dak., since 1974.

Sowing juniper seed adjacent to beds containing juniper stock should be avoided, if possible, so as to reduce chances of spores from infected older stock infecting new seedlings. Junipers or other hosts of this fungus should not be used in nursery windbreaks or in landscape plantings on nursery ground, because they may be a source of inoculum (spores) for nursery stock. Such trees are likely to be infected extensively if pruning results in development of juvenile foliage.

Poorly drained areas also should be avoided, because losses are often greater where water tends to pool (fig. 6-10). Overhead sprinkler irrigation should be terminated in time for free water to evaporate from foliage before dusk. Because shading frames increase the time that water remains on foliage, they should not be used unless absolutely necessary.

Phomopsis blight is particularly difficult to control in the highly moist conditions required for production of juniper grafts. Watering can disperse spores present on scions or understocks, and the long periods when free water is present on the foliage favors infection. Under these highly moist conditions, the most effective fungicides are apt to fail. The nurseryman has to obtain a balance in the moisture regime so that graft production will be successful, and Phomopsis infection will not occur. This is especially difficult if grafts are produced in enclosures in which temperatures are moderate and water is applied at frequent intervals by mist systems.

Some nurseries have abandoned production of highly susceptible cultivars (i.e. *Juniperus sabina tamariscifolia*) because of continued high losses. *Phomopsis juniperovora* can cause unsightly junipers in landscapes but seldom kills established trees (fig. 6-11). The objective of Phomopsis control in landscapes is to reduce the unsightly conditions. Infection of outplanted junipers can be severe during unusually moist growing seasons, but infection is usually moderate in most years. Infection can be reduced by restricting pruning and shearing to periods when the resulting flush of new growth will occur during the drier part of the growing season. Junipers are sometimes pruned after the first flush of growth in the spring; this can result in a new flush of growth in early summer, when rain may be plentiful. Such new growth is especially vulnerable to infection.

Fungicides can be used for control of *P. juniperovora* in landscapes, although tests have not been made to define the most effective and economical spray schedules. Frequent applications of fungicide would be impractical in outplantings, but applying fungicide during the early and late flushes of growth is practical and probably would be adequate in most years.

Physiology and Morphology

Spores are extruded from pycnidia in tendrils or globules. Globules usually form when free water is present on tissues containing pycnidia. Temperature affects the rate at which spores are extruded from pycnidia. On branches kept in the dark at 100% relative humidity, spores were extruded within: 23 hours at 24°C and 28°C; 30 hours at 20°C; 45 hours at 16°C; and 93 hours at 12°C. Spores were not extruded at either 32° or 36°C, after 165 hours. Spores were extruded at similar rates whether pycnidia-bearing tissues were incubated in light or dark at 24°C or 28°C and 100% relative humidity.

Spores in tendrils are tightly bound by a matrix. Considerable agitation is required to disperse spores in tendrils placed in water. Spores were not dispersed after 7 hours when tendrils were placed in water and not agitated.

Alpha spores germinated over the temperature range 12° to 32°C when incubated for 18 hours on water agar (fig. 6-12). Spores germinated at 8°C after incubation for 34 hours but not after 18 hours. More than 60% of the spores germinated over the range 12° to 32°C.

Germ tube growth was greatest at 26°C (fig. 6-12). Germ tubes were evident 4 hours after incubation started. Germ tubes developed slowly from 4 to 12 hours; from 12 to 28 hours, development was rapid and nearly linear with time (fig. 6-13). Germ tube development was better on water agar and cornmeal sucrose agar than on potato dextrose agar. Germ tubes grew more rapidly (44 μm versus 10 μm) and percent germination was higher (100% versus 15%) when spores were incubated on water agar than when incubated in distilled water, after 18 hours, at 24°C.

Percentage spore germination and germ tube lengths were similar whether spores germinated in the dark or in incandescent or fluorescent light.

Spores obtained from tendrils that had been exposed to temperatures of 1°. 10° and 24°C for 24 hours germinated 100%; exposure at 33-43°C resulted in 80% germination and germ tubes about one-half as long (24 μm) as at the lower temperatures. Spores subjected to -22°C in water or in tendrils still germinated.

Spores which had been hydrated, then dried at temperatures ranging from 4° to 54°C, still germinated. Increase in temperature or length of drying period decreased percent germination and germ tube lengths.

Growth of *P. juniperovora* on agar media was optimum at 24-26°C (fig. 6-14). The rate of growth from 3 to 9 days was linear with time. Growth was greater on potato dextrose agar and cornmeal sucrose agar than on prune agar and malt extract agar (fig. 6-15). Colony diameters of 27 isolates, after 6 days, at 24°C, on cornmeal sucrose agar ranged from 5.3 to 8.0 cm. Seventeen isolates had colony diameters between 7 and 8 cm. Growth was as rapid in the dark at it was in the light (1075 lux).

All isolates developed a yellow color in advance of the colony periphery. Color intensity varied among isolates. The color intensity of all isolates was the same whether grown in light or dark. Orange-red crystals formed in all media. The major constituent of the orange-red crystals is a tetrahydroquinone (Wheeler, Wheeler, and Peterson 1975) which was previously isolated by Stoessl (1967) and named by him altersolanol A.

Pycnidia were not produced in abundance on these media, even when cultures were incubated in the light. Excellent pycnidial production was obtained using asparagine agar with sucrose as the carbon source.

Asparagine Agar

KH_2PO_4	1.0 g
$MgSO_4.7H_2O$	0.5 g
Asparagine	2.3 g
Agar (Difco Noble Agar)	20.0 g
Sucrose	10.0 g
Distilled water	1.0 l

Light (280 lux) was required for pycnidial production. Production of pycnidia with fertile spores was extensive with 3 to 4 weeks incubation at 24°C. Production was better with sucrose than with glucose, fructose, lactose, or mannitol. Production using sucrose at 10 g/l or 20 g/l was better than using 2 g/l sucrose.

Infection of Seedlings under Controlled Conditions

Seedlings of *J. virginiana* and *J. scopulorum*, inoculated with spore suspensions and incubated at temperatures ranging from 16° to 32°C (100% relative humidity), were readily infected. Infection at 12°C was very light. Intensity of infection was greater at 24°C to 28°C than at other temperatures.

Seedlings became infected after only 7 hours incubation at 24°C and 100% relative humidity. The amount of infection was similar whether inoculated plants were incubated in the dark or in the light (2-day continuous fluorescent, 12,900 lux). After incubation for 2 days at 24°C, disease development was enhanced by higher post-incubation temperatures (28-32°C). The level of infection with 7 to 9 hours incubation was only 21% of level of infection with 24 hours incubation. Infection levels after 1, 2, or 3 days of incubation were similar; however, the level of infection was 50% less when both *J. virginiana* and *J. scopulorum* were incubated for 4 days.

The information on inoculations with *P. juniperovora* is being used to evaluate resistance among progenies of 86 select eastern redcedar trees located in the Great Plains. Resistance to *P. juniperovora* is present within eastern redcedar (fig. 6-16). Research is seeking to determine if there is genetic resistance which can be utilized to reduce the impact of this fungus on eastern redcedar seedlings in nurseries.

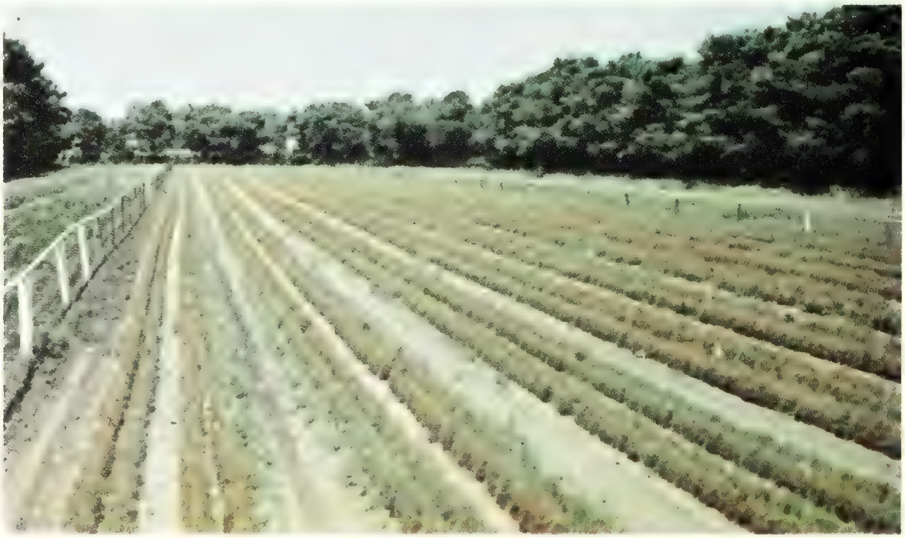

Figure 6-1.—Damage by *Phomopsis juniperovora* to second-year eastern redcedar seedlings.

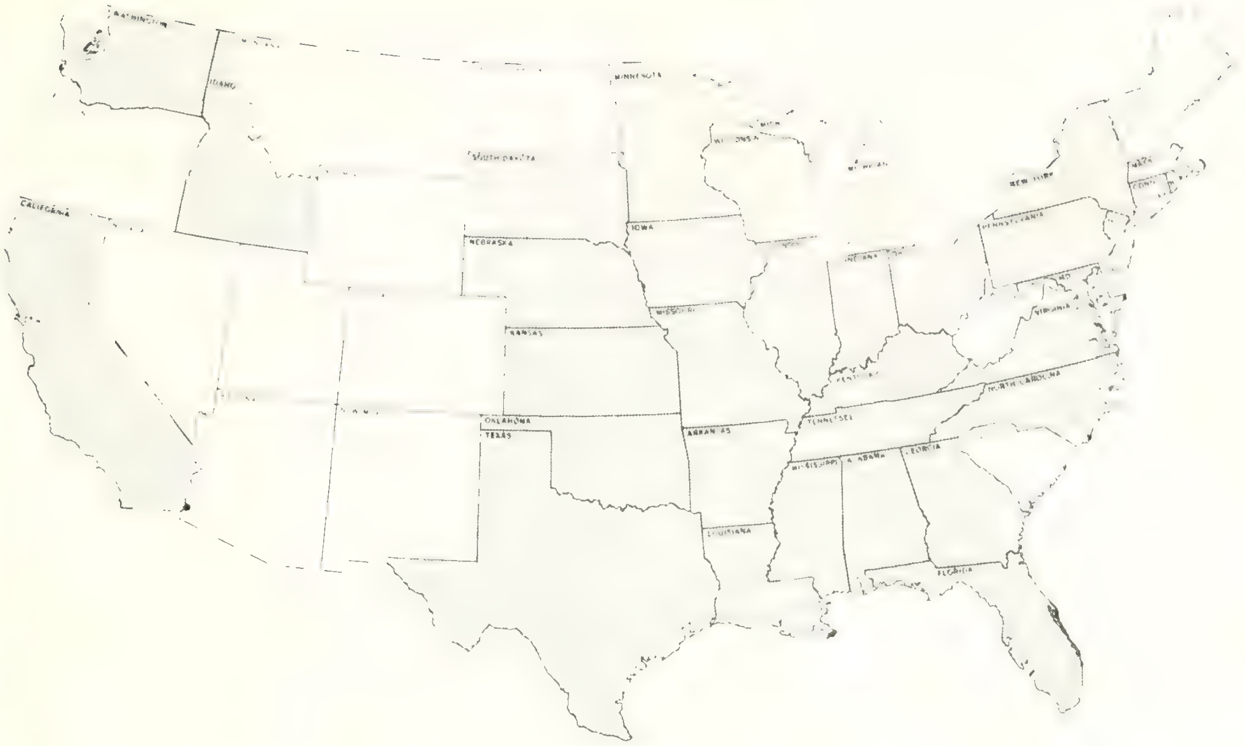

Figure 6-2.—*Phomopsis juniperovora* occurs in shaded states.

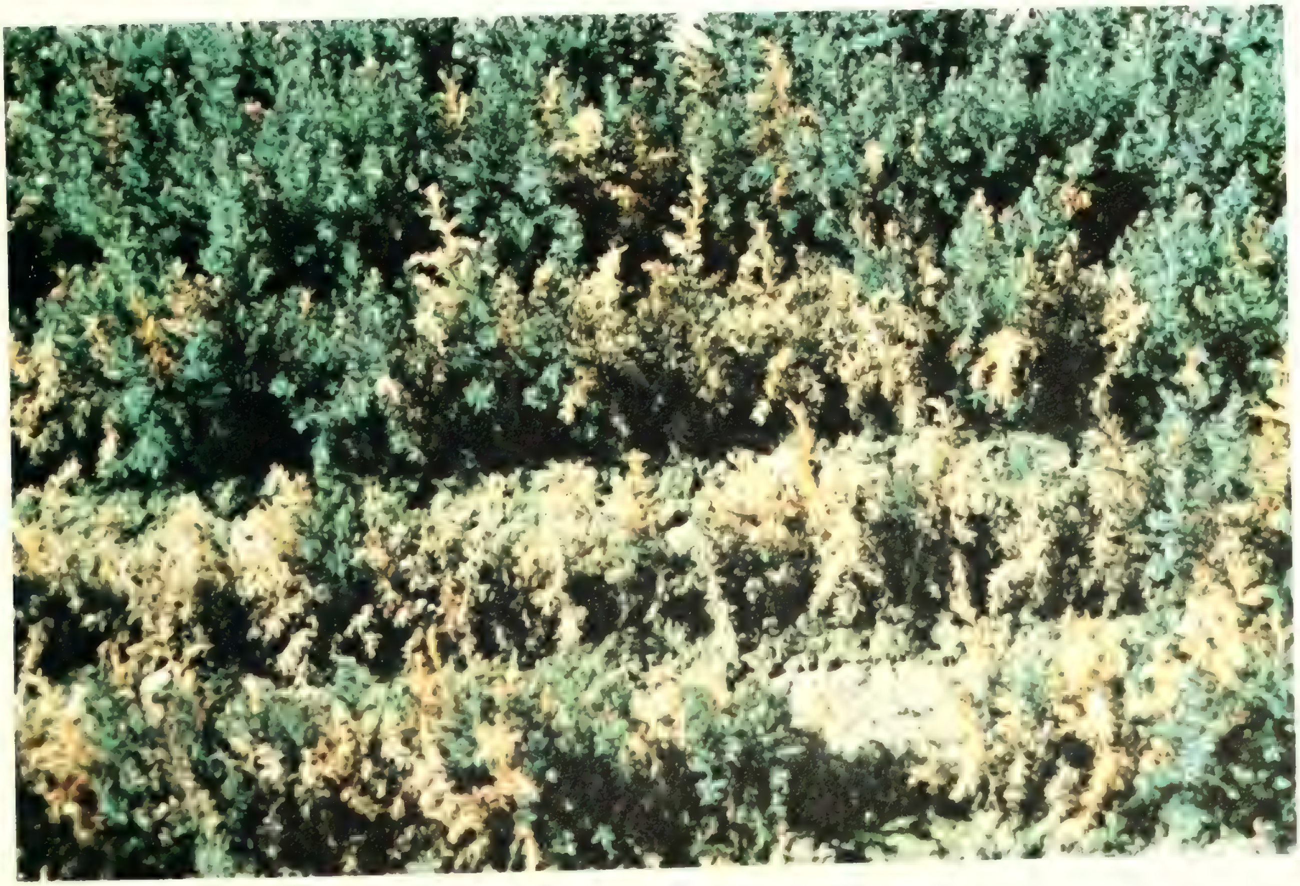

Figure 6-3.—Stem and branch tips of second-year eastern redcedar seedlings killed by *Phomopsis juniperovora*.

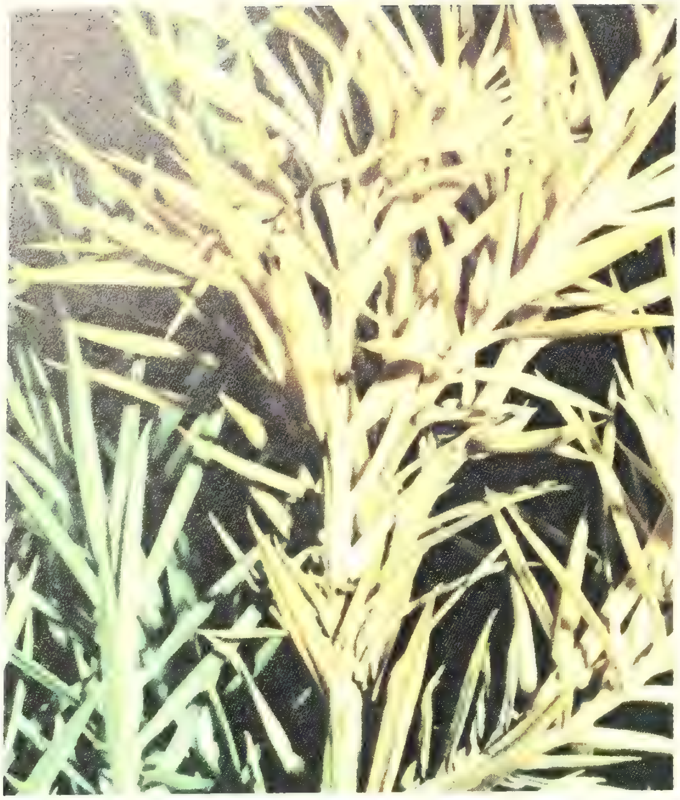

Figure 6-4.—Typical damage caused by *Phomopsis juniperovora* —dead reddish tops with ashen grey tissues where stem girdled.

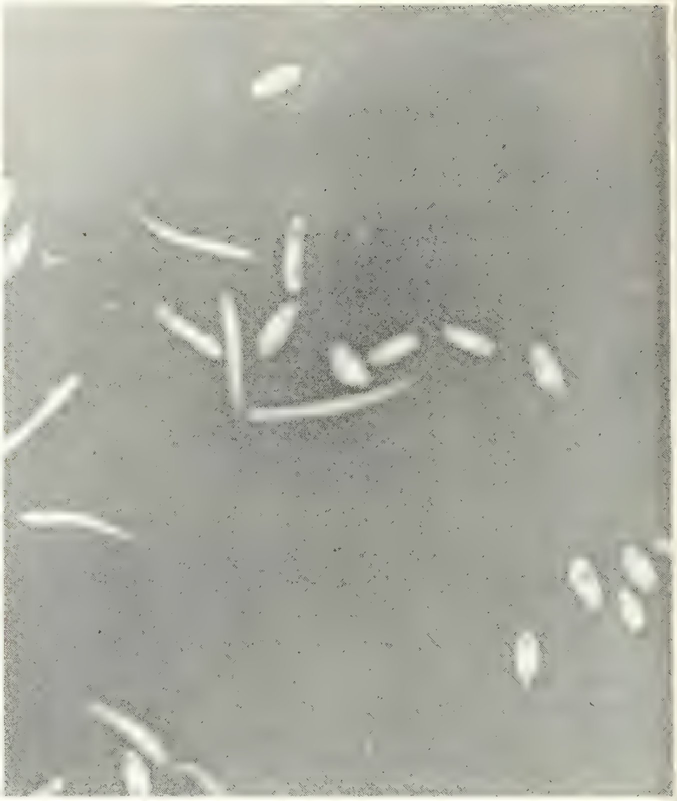

Figure 6-6.—Alpha (short) spores and beta (long) spores of *Phomopsis juniperovora*. Alpha spores have two oil globules.

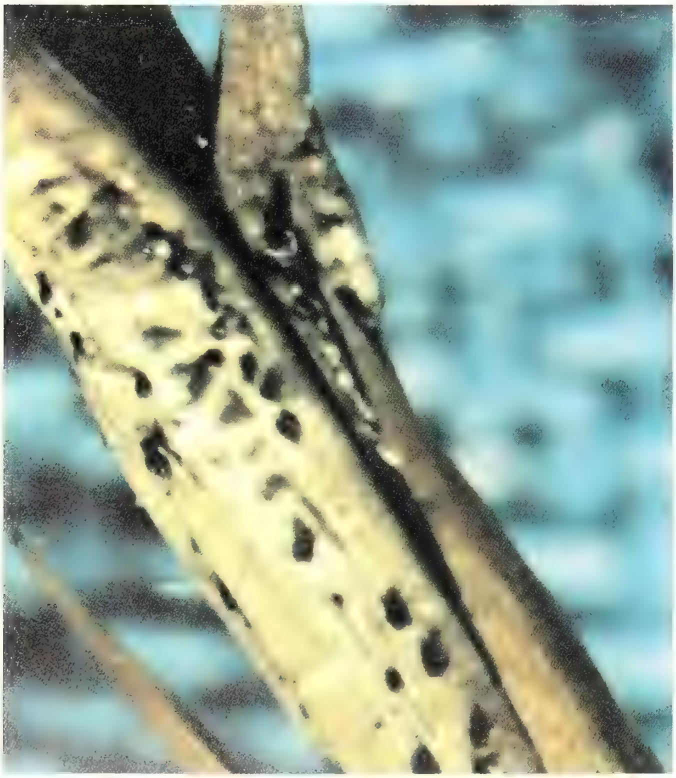

Figure 6-5.—Black fruiting bodies (pycnidia) of *Phomopsis juniperovora* on stem and leaf of eastern redcedar.

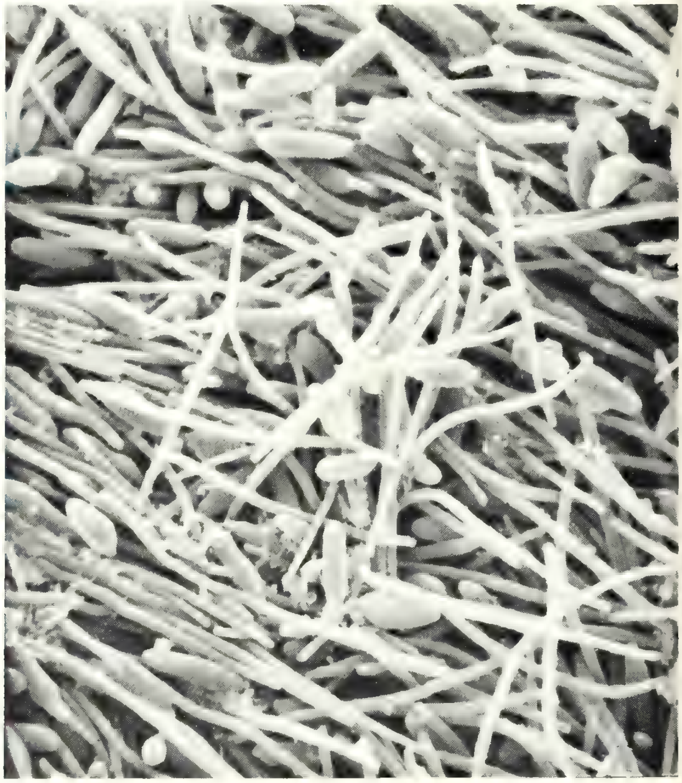

Figure 6-7.—Alpha and beta spores of *Phomopsis juniperovora* magnified 2000 times.

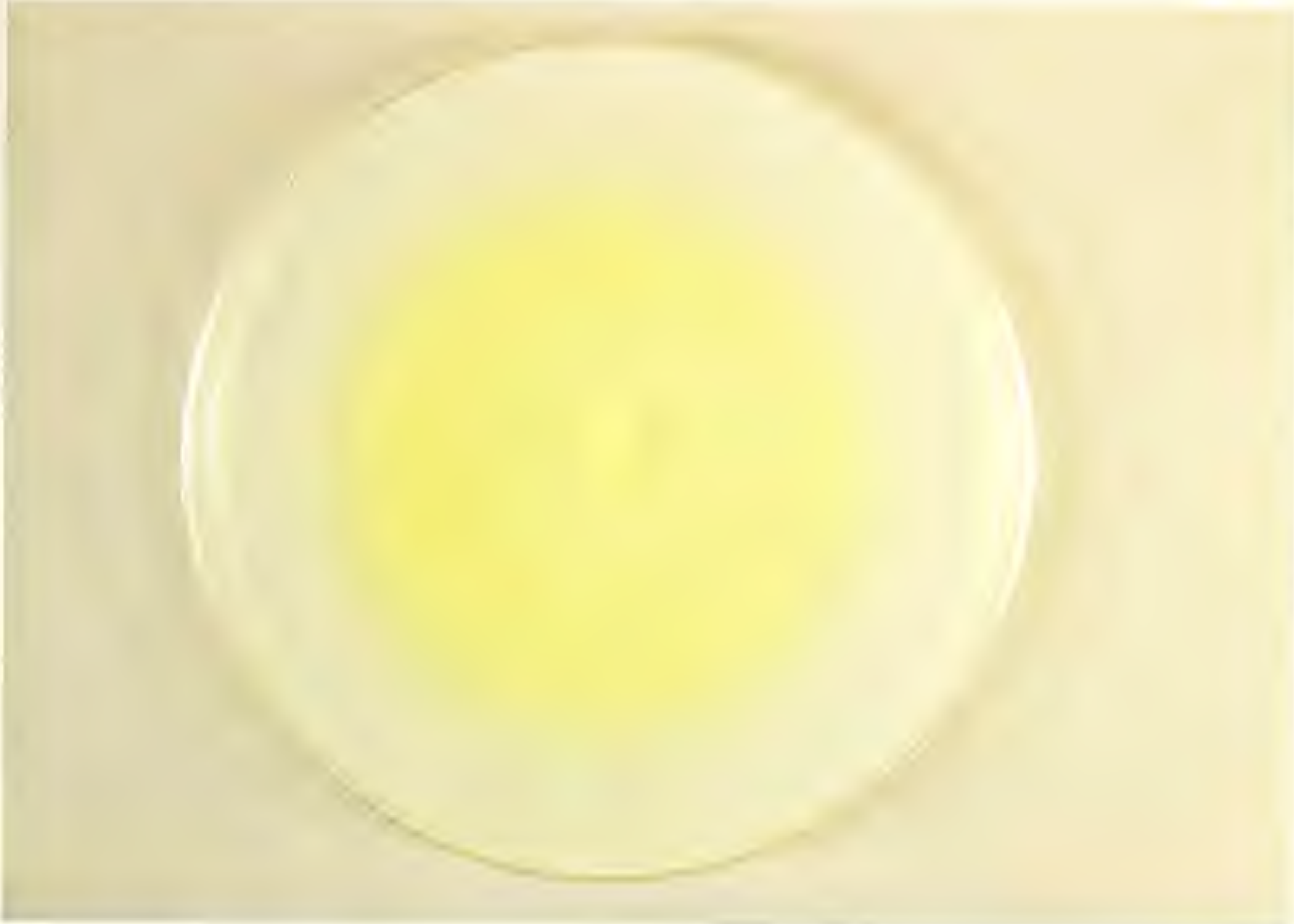

Figure 6-8.—Typical yellow coloration of *Phomopsis juniperovora* colony.

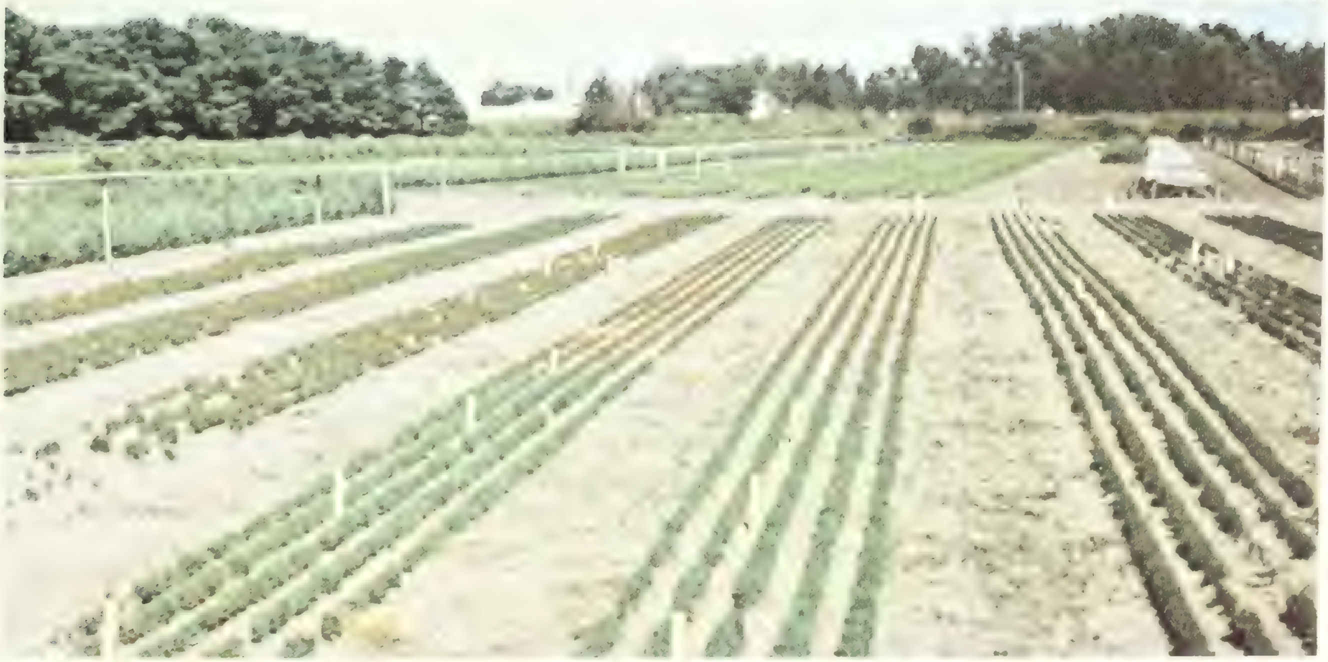

Figure 6-9.—Control of Phomopsis blight of eastern redcedar seedlings by a protective fungicide (foreground); unsprayed seedlings in background.

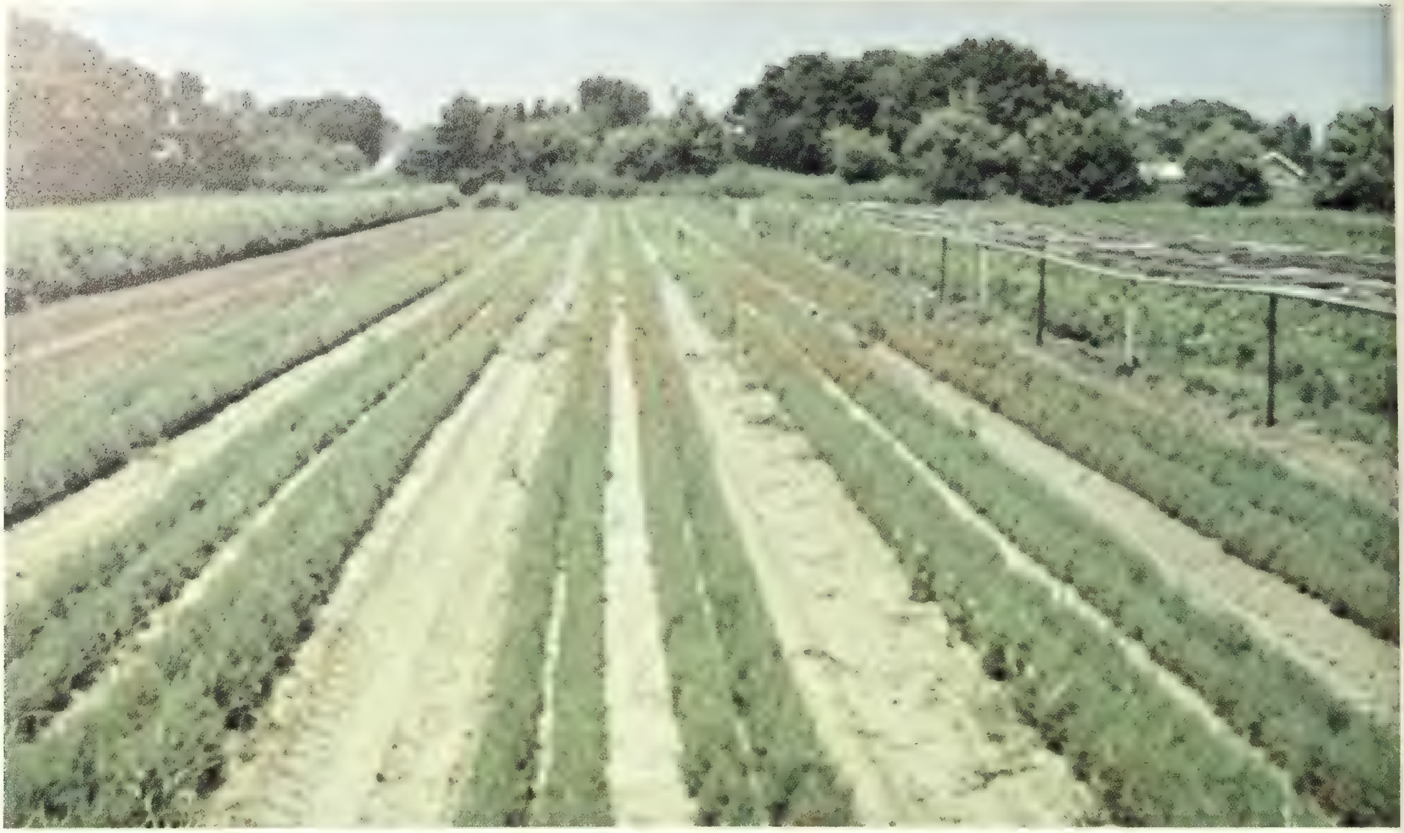

Figure 6-10.—Severe infection by *Phomopsis juniperovora* in a poorly drained (low) area in the nursery.

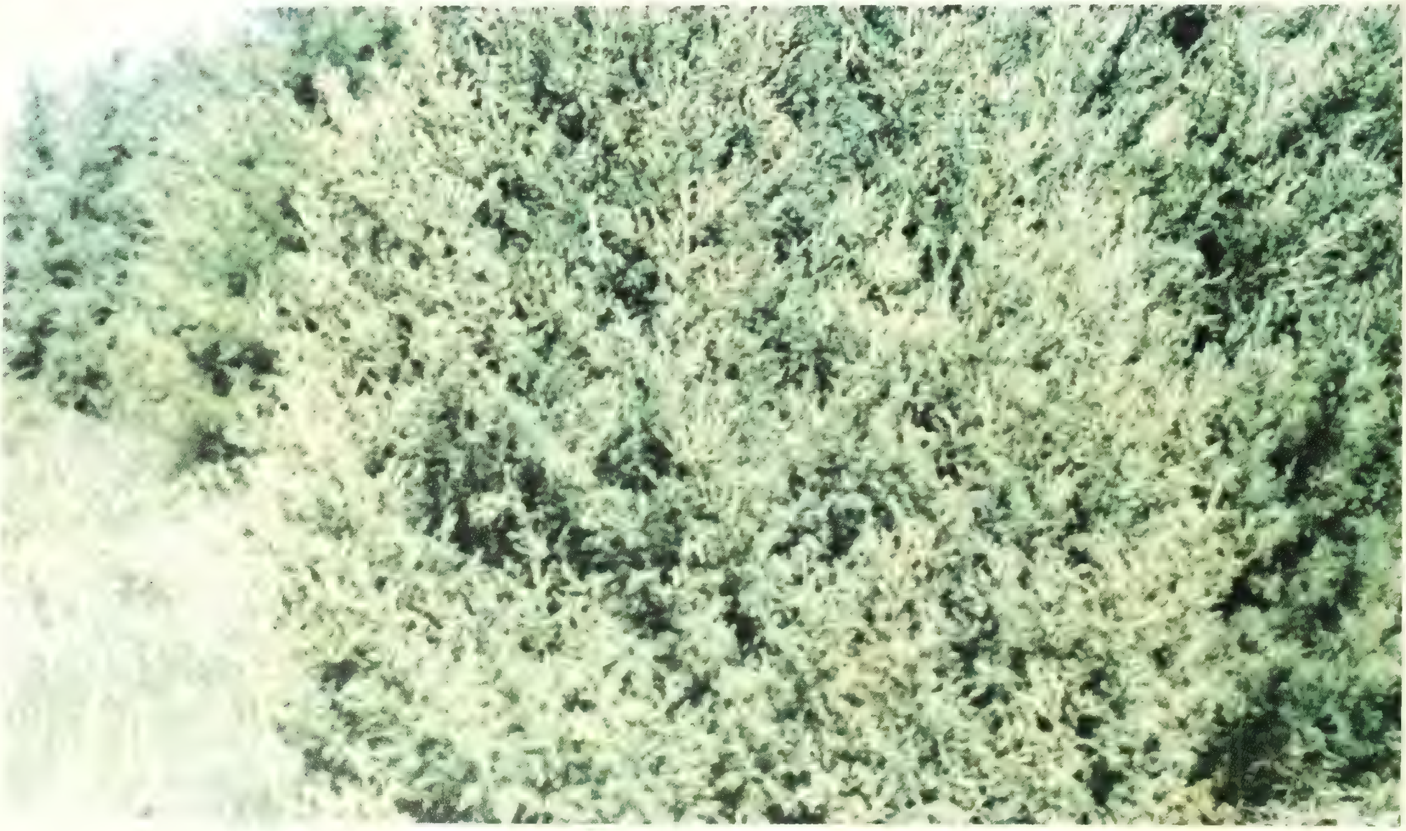

Figure 6-11.—Eastern redcedar in a 7-year-old planting with branch tips infected by *Phomopsis juniperovora.*

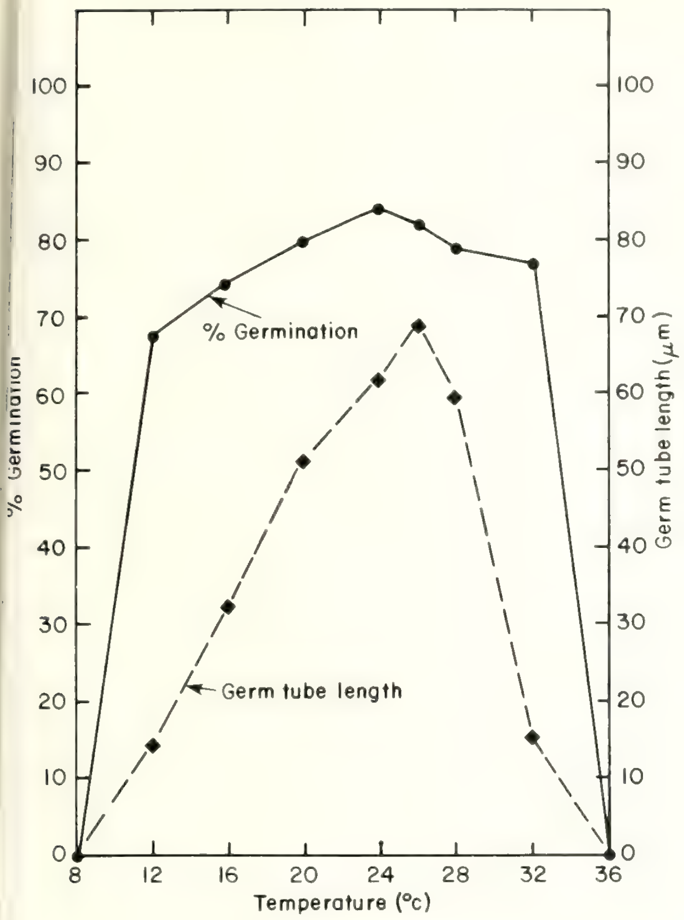

Figure 6-12.—Effect of temperature on germination of spores of *Phomopsis juniperovora* incubated for 18 hours on water agar.

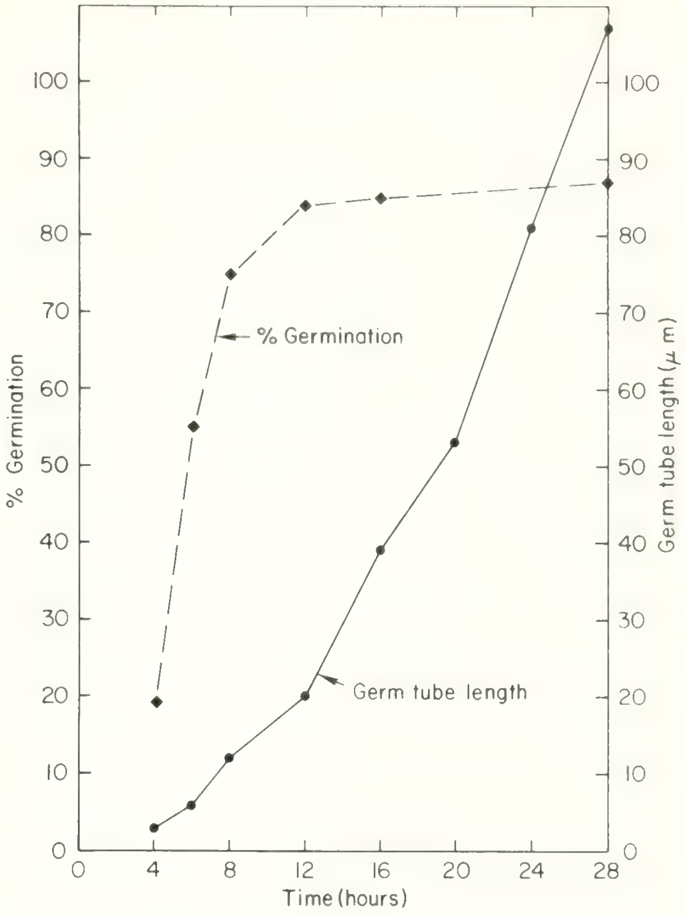

Figure 6-13.—Germ tube length and percent germination of *Phomopsis juniperovora* spores incubated for various periods of time, at 24°C, on water agar.

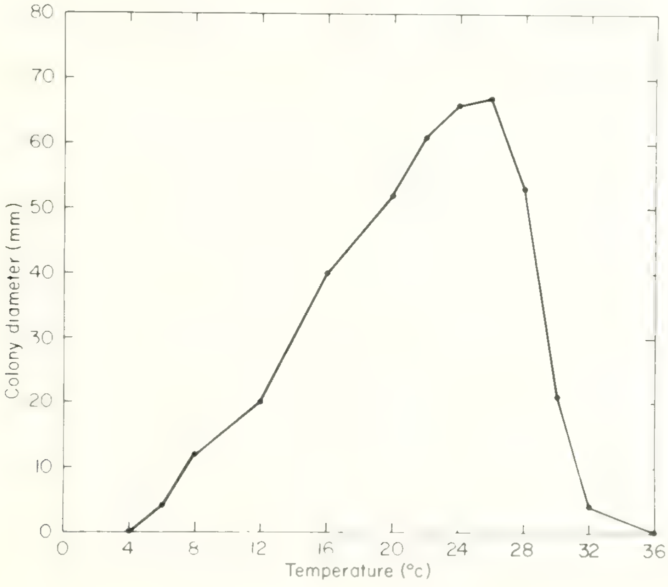

Figure 6-14.—Effect of temperature on colony diameter of *Phomopsis juniperovora* grown for 6 days on corn meal sucrose agar.

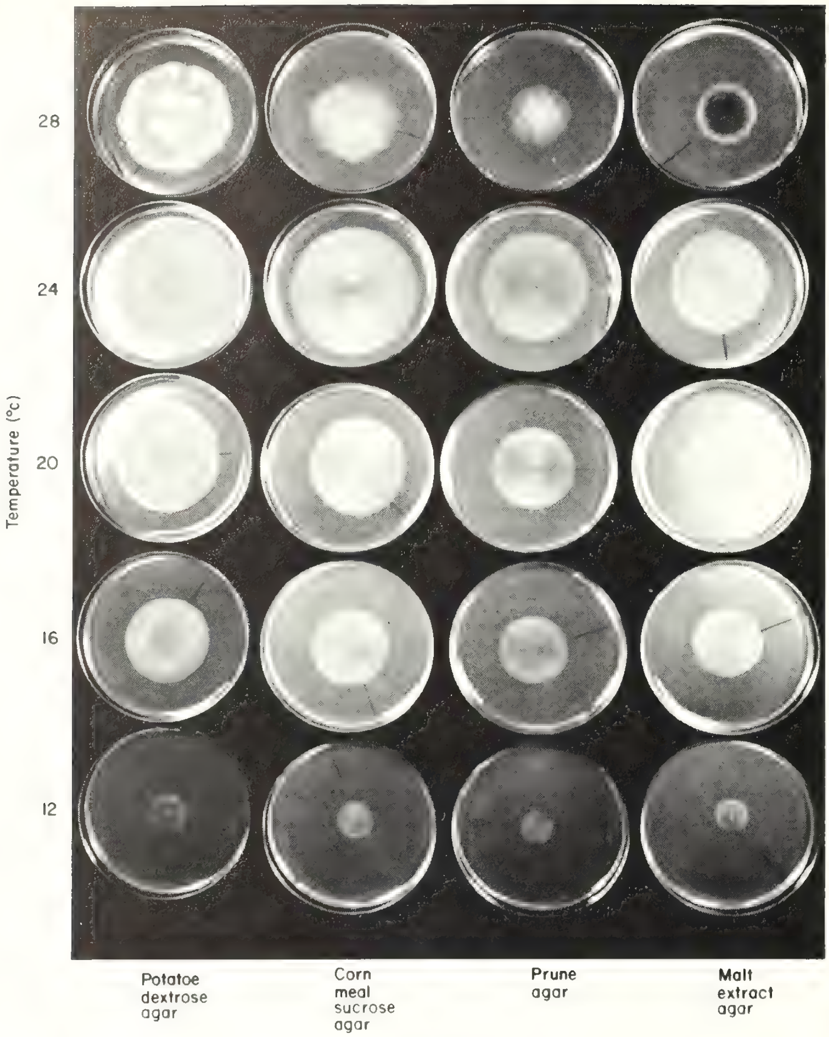

Figure 6-15.—Effect of temperature and cultural media on appearance and growth of *Phomopsis juniperovora* colonies after 6 days.

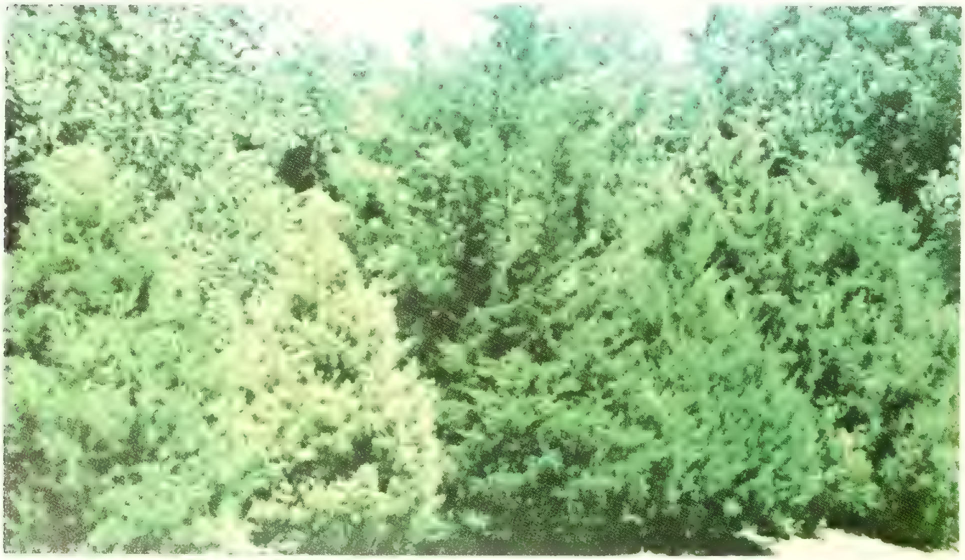

Figure 6-16.—Resistant eastern redcedar trees adjacent to a tree severely infected by *Phomopsis juniperovora*.

7. Cercospora Blight of Junipers

Junipers are damaged by the fungus *Cercospora sequoiae* and the related fungus *Cercospora sequoiae* var. *juniperi*. In the Great Plains, *C. sequoiae* var. *uniperi* has severely damaged *Juniperus virginiana* and *J. scopulorum* in well established windbreaks and other plantings (fig. 7-1). Several successive seasons of nfection can kill trees. The distribution of these two fungi in the United States is shown in figure 7-2.

This fungus has not been a threat to production of uniper seedlings in the Great Plains; it is seldom found on nursery seedlings. However, Cercospora infection has been commonly observed in nurseries on grafted selections of junipers, particularly selections of *J. scopulorum* that have been kept in the nursery for 5 or 6 years.

Diagnosis

Cercospora blight is easier to diagnose than Phomopsis and Kabatina blights of junipers. The branches of Cercospora infected trees usually will be devoid of foliage near their bases but will have healthy foliage on their tips (fig. 7-1); whereas, the branches of Phomopsis and Kabatina infected trees will have dead tips.

Juniper foliage has been grouped into three types: (1) whip leaves characteristic of long shoot growth on the ends of secondary and tertiary branches; (2) spur leaves characteristic of short (spur) branches; and (3) juvenile leaves characteristic of seedlings.

Early symptoms are bronzed tips of leaves on spur shoots. Subsequently these leaves become entirely bronzed, then necrotic. Commonly, all leaves of a branchlet are affected. Infected foliage on branchlets usually dies in late September.

Affected branchlets drop from trees in October and November, resulting in the typical appearance of diseased trees—the extremities of the branches bear healthy green foliage and the inner crown is devoid of foliage. Following severe infection, juvenile foliage commonly develops on branches which previously have had only spur and whip foliage.

Life Cycle

Spores of the fungus are dispersed from late April through October. Dispersal may not be abundant until late May or June, and no spores are dispersed during rainless periods. There is little or no long-distance dispersal of spores; no spores were collected in traps located within 6 feet of severely infected trees. There is considerable yearly variation in the amount of infection. Infection has been severe when rainfall during the growing season was at or above average. Infection was slight during the drought years of 1975 and 1976 in eastern Nebraska. Moisture is required for spores to disperse and germinate and for the fungus to penetrate foliage.

Junipers in eastern Nebraska are first infected in early to midsummer. Initial infection occurred during the period July 14 to 28, 1971 and June 21 to July 5, 1972. On spur leaves, symptoms first were observed August 8, 1971 and July 19, 1972. The period between initial infection and first appearance of symptoms is between 2 and 3 weeks.

On juvenile foliage, symptoms were first evident July 19, 1972; by September 26, most of the infected leaves were necrotic. By October 3 necrosis was extreme. This indicates that the disease develops more rapidly in juvenile leaves than in spur leaves. Also, both current-year and previous-years' juvenile leaves became infected, whereas only the previous-years' spur leaves became infected.

Fruiting bodies (sporodochia) (figs. 7-3, 7-4) resulting from current-season's infection were observed in spur foliage September 26, 1974. They sporulated readily when incubated at 24°C and 100% relative humidity for 18 hours. In 1973, sporodochia first were found on spur foliage collected in September. Sporodochia first were found September 5, 1972 on juvenile leaves infected that year.

Tips of secondary and tertiary branches on 10-year-old *J. virginiana* were free of infection for an average distance of 45 cm. Measurements of the distance between the disease-free ends of these branches and the limit of infection of 1971 revealed that the disease had extended an average distance of 28 cm along the branches in 1972. Lack of infection on tips may be a result of less moisture on the outermost foliage because of more rapid drying. Whip foliage which develops on branch tips also may be resistant to infection.

Trees planted in north-south rows had much more infection on the west side than on the east side. The longer persistence of moisture from dew or evening rains on the west side probably accounts for the higher levels of infection.

The disease develops more rapidly in *J. scopulorum* than in *J. virginiana* (fig. 7-5). In a shelterbelt containing a row of both species, 91% of the *J. scopulorum* died, compared to 41% of the *J. virginiana*. The fungus killed more *J. scopulorum* (fig. 7-6) and *J. monosperma* than *J. virginiana*, in a conifer test planting near Mapleton, Iowa.

Control

Because trees with whip and spur foliage were not infected before late June (and then only previous years' foliage became infected), a highly persistent fungicide applied before late June, theoretically, could protect trees with spur and whip foliage for the entire season. Because of fungicide weathering, however, an additional application in late July usually is required.

Because both current-year and previous years' juvenile foliage become infected, juniper trees containing juvenile leaves would require additional fungicide applications to protect newly developing juvenile leaves. Bordeaux mixture (8-8-100) provided a high degree of control in tests.

Park managers using control procedures outlined (fig. 7-7) have controlled the Cercospora blight fungus on *J. scopulorum* and on *J. virginiana* since 1973. The timing of fungicide applications shown in figure 7-7 was developed from tests in eastern Nebraska. Timing should be modified slightly in other areas—earlier application in southern locations, and later applications in northern locations.

Cercospora blight is found more frequently in new plantings of *J. scopulorum* than in new plantings of *J. virginiana*. Where Cercospora may be a problem, it would be better to plant *J. virginiana*.

Variation in resistance to cultivars of these two junipers species has not been systematically evaluated. To determine whether there is usable genetic resistance to Cercospora, a test planting of progenies from 158 select trees in the Great Plains, was made in eastern Nebraska, in 1980. Results from this test should be available in the early 1980's.

Physiology and Morphology

Growth of the fungus in malt extract broth was greatest at 24°C (fig. 7-8).

More than 90% of spores germinated on water agar within 24 hours, over the range 16° to 28°C; no spores germinated at 8°C or 32°C (fig. 7-9). Germ tube growth was greatest at 24-26°C (fig. 7-9). Germination began within 6 hours at 24°C, and percent germination was near maximum within 16 hours (fig. 7-10). Percent germination and germ tube lengths were similar whether spores were incubated (24°C) in the dark or in the light.

The age of cultures from which spores were obtained strongly influenced spore germination and germ tube growth. After incubation for 24 hours at 24°C, germination and germ tube lengths for spores from 7-day-old cultures were 91% and 47 μm, from 10-day-old cultures 57% and 22 μm, and from 14-day-old cultures 16% and 10 μm, respectively. Spores were produced in quantity on carrot-leaf decoction agar (Kilpatrick and Johnson, 1956) when incubated under continuous fluorescent light (624 lux).

Spores are cylindrical, olive brown, slightly spiny, 1-7 septate (mostly 5-6) (figs. 7-11, 7-12). Spores ranged from 16.5-69.5 μm by 2.0-3.6 μm, and averaged 40.8 by 3.1 μm. Spores are borne at the apex of the conidiophores, and on new growing points which develop just below and to one side of the previously developed spore.

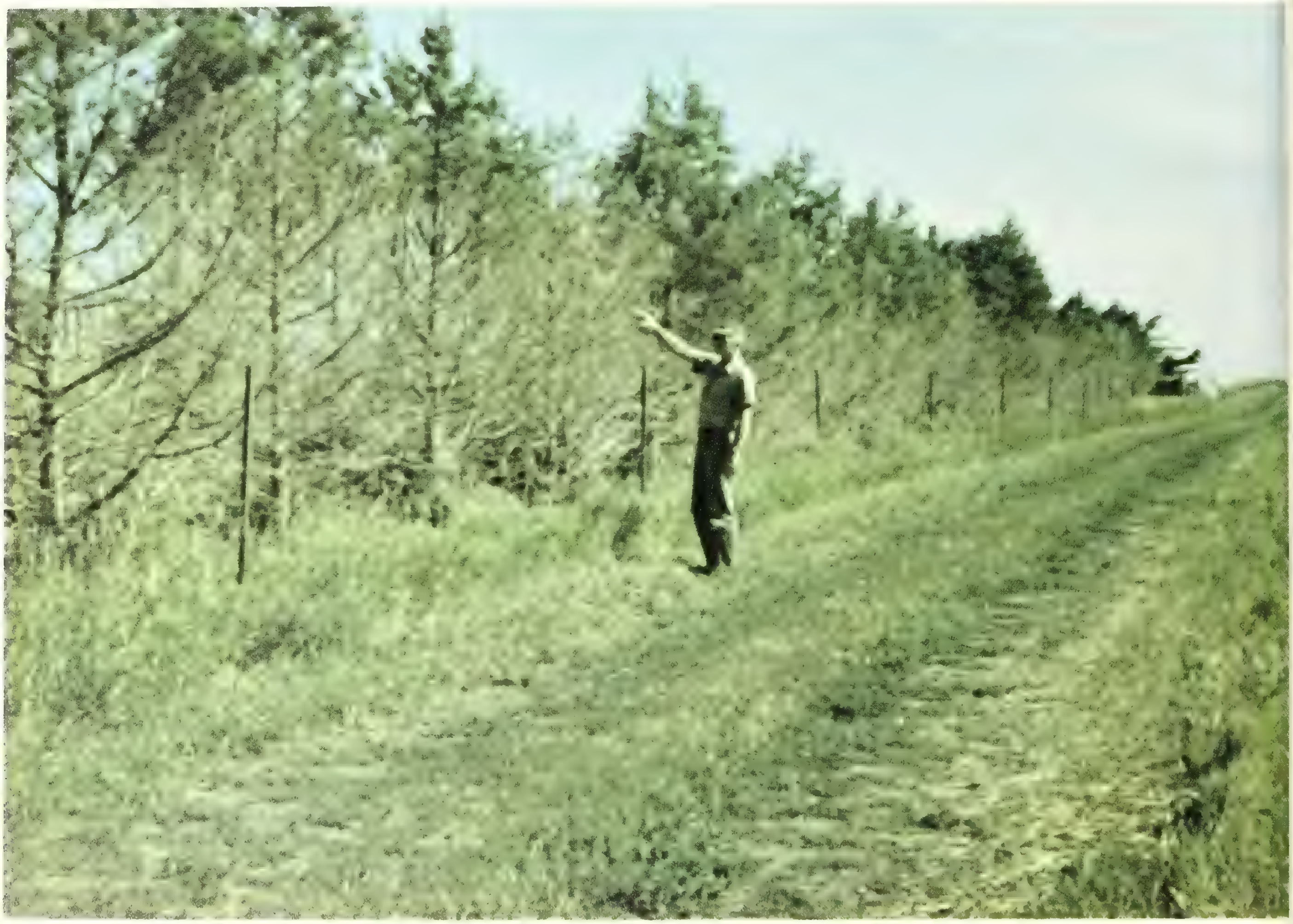

Figure 7-1.—Typical appearance of Rocky Mountain juniper severely damaged by *Cercospora sequoiae* var. *juniperi*.

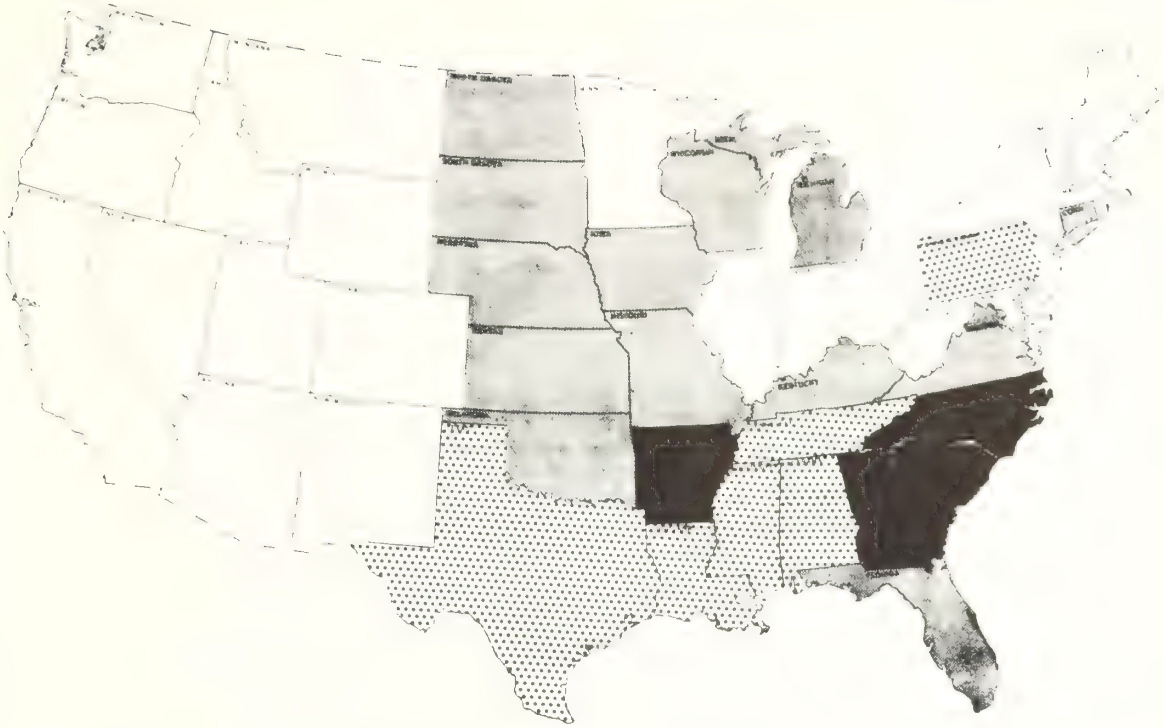

Figure 7-2.—Geographic distribution of *Cercospora sequoiae* and *Cercospora sequoiae* var. *juniperi*. *Cercospora sequoiae* (dots); *Cercospora sequoiae* var. juniperi (gray); both (black).

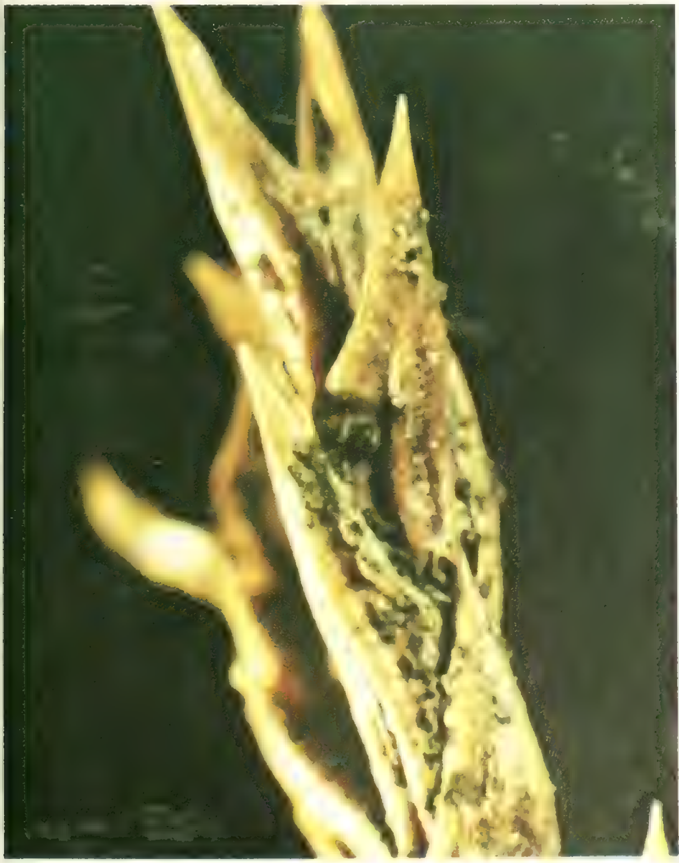

Figure 7-3.—Dark fruiting bodies of *Cercospora sequoiae* var. *juniperi* on Rocky Mountain juniper foliage.

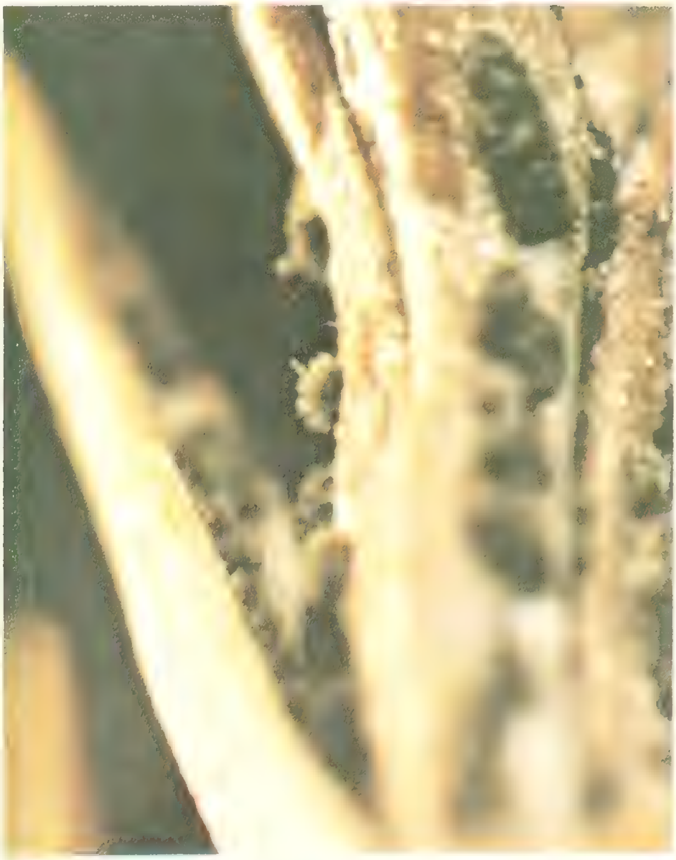

Figure 7-4.—Closeup of fruiting bodies of *Cercospora sequoiae* var. *juniperi* showing fuzzy gray appearance of conidia and conidiophores.

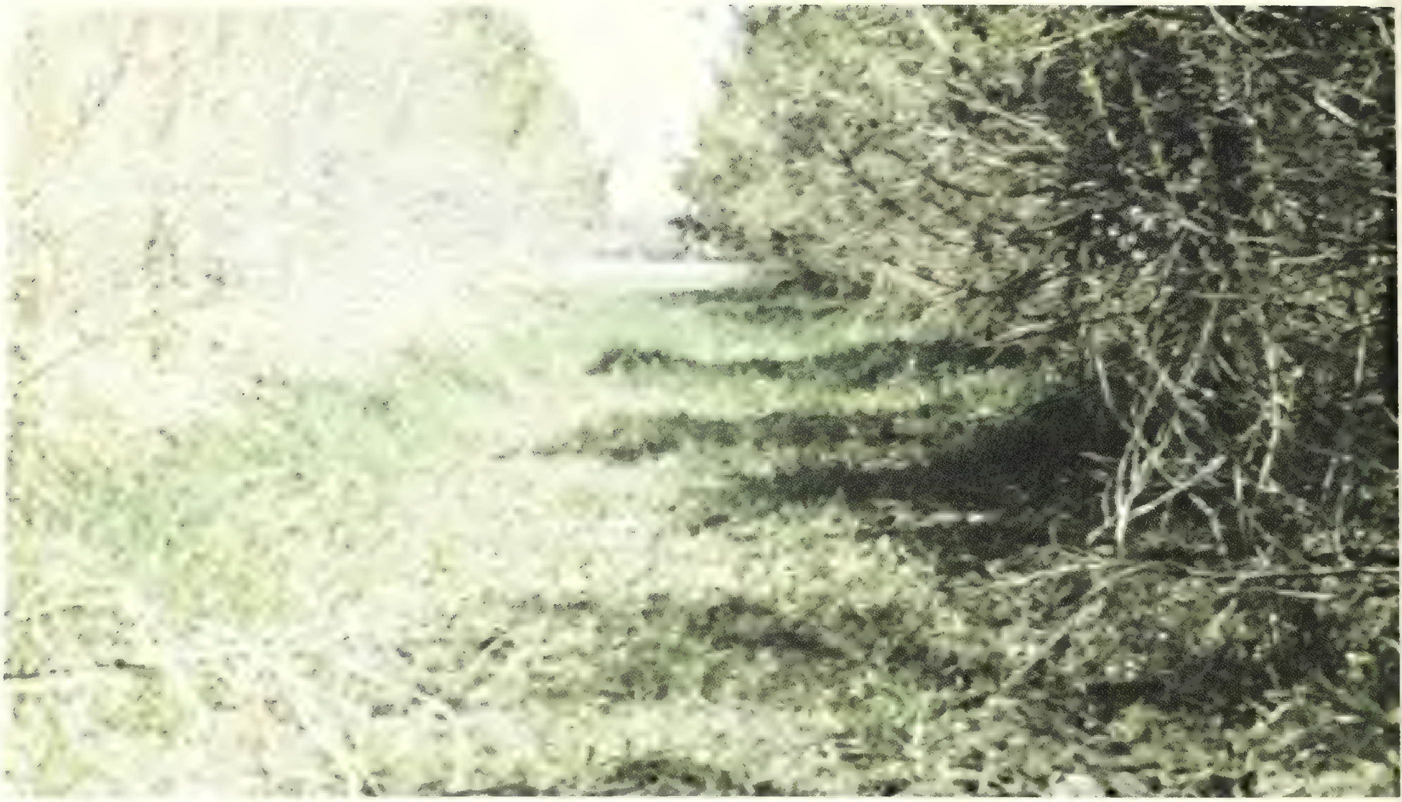

Figure 7-5.—Damage by *Cercospora sequoiae* var. *juniperi*; damage is more severe to Rocky Mountain juniper (left) than to eastern redcedar (right), in an eastern Nebraska windbreak.

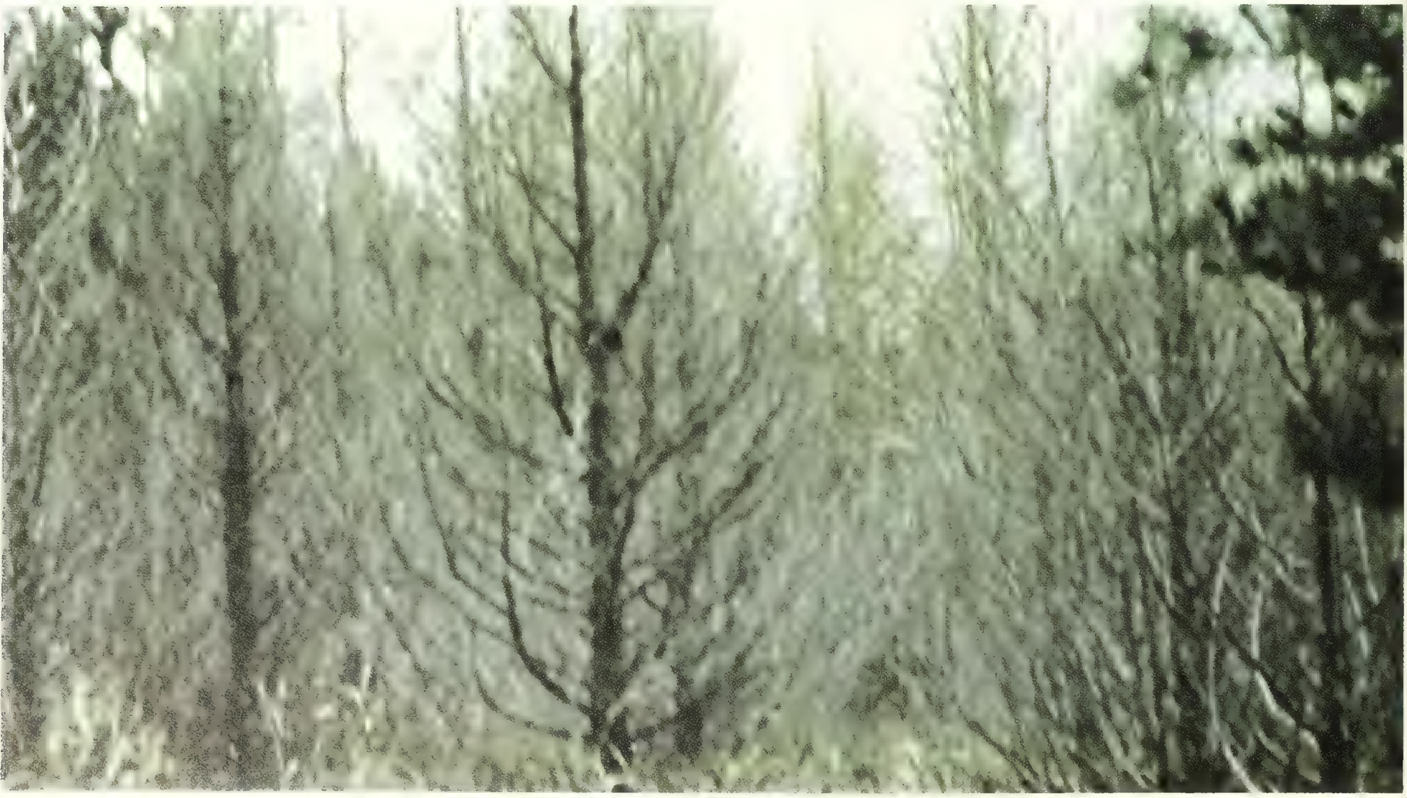

Figure 7-6.—A Rocky Mountain juniper planting in western Iowa destroyed by *Cercospora sequoiae* var. *juniperi*.

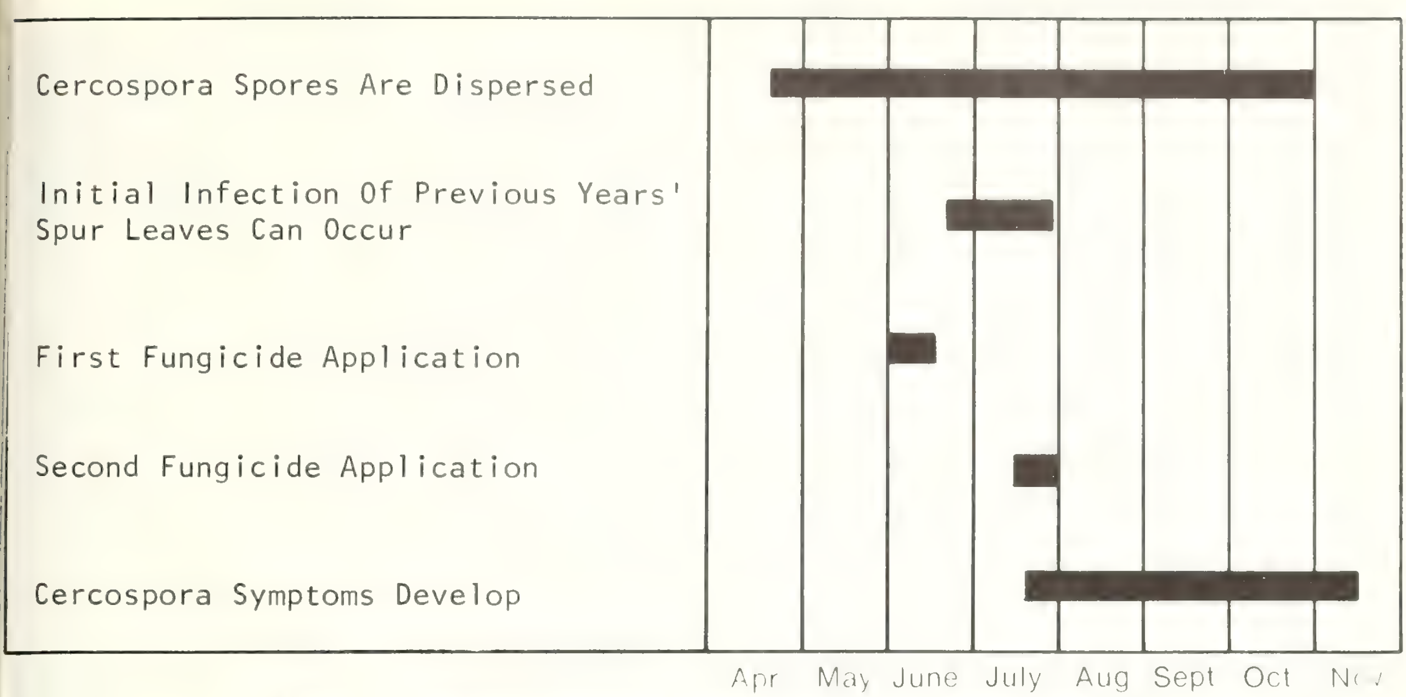

Figure 7-7.—Schedule for developing programs for control of Cecospora blight.

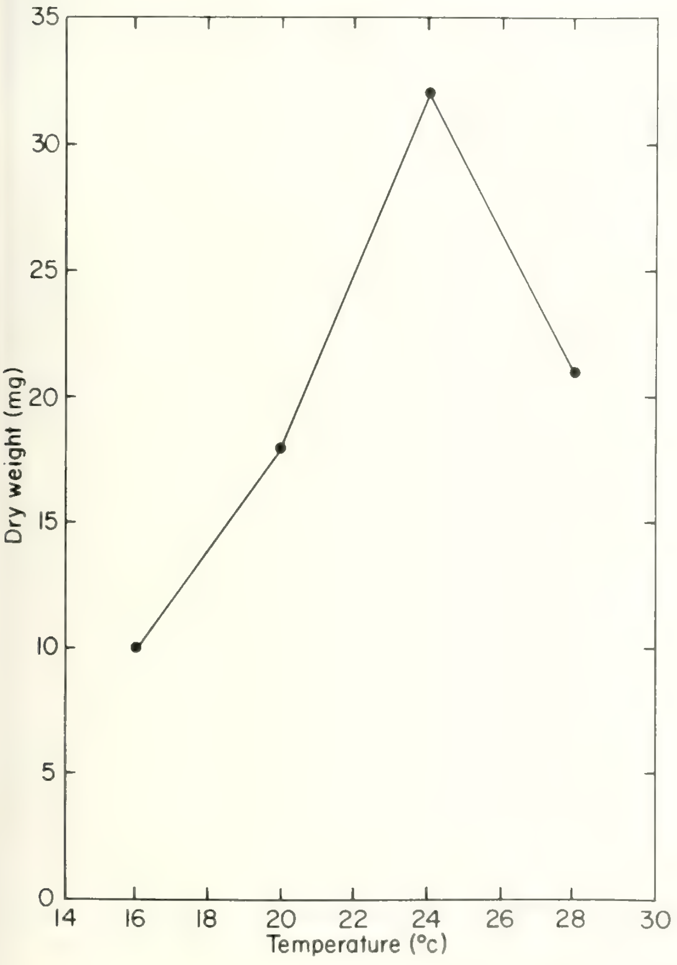

Figure 7-8.—Effect of temperature on growth of *Cercospora sequoiae* var. *juniperi* in a liquid culture medium, after 14 days.

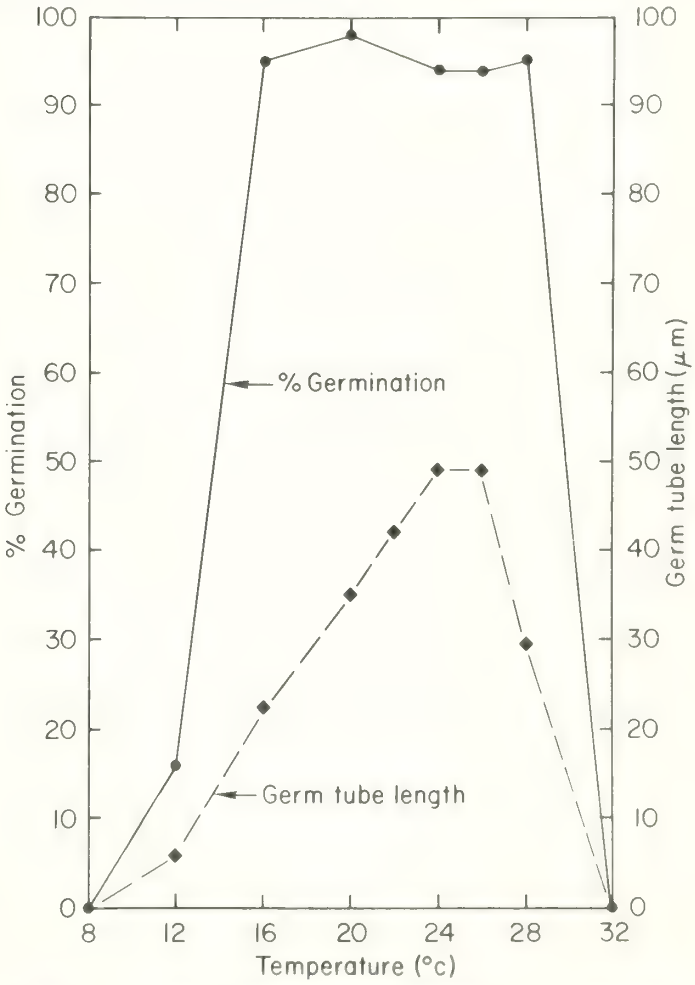

Figure 7-9.—Effect of temperature on germination of *Cercospora sequoiae* var. *juniperi* spores incubated for 24 hours on water agar.

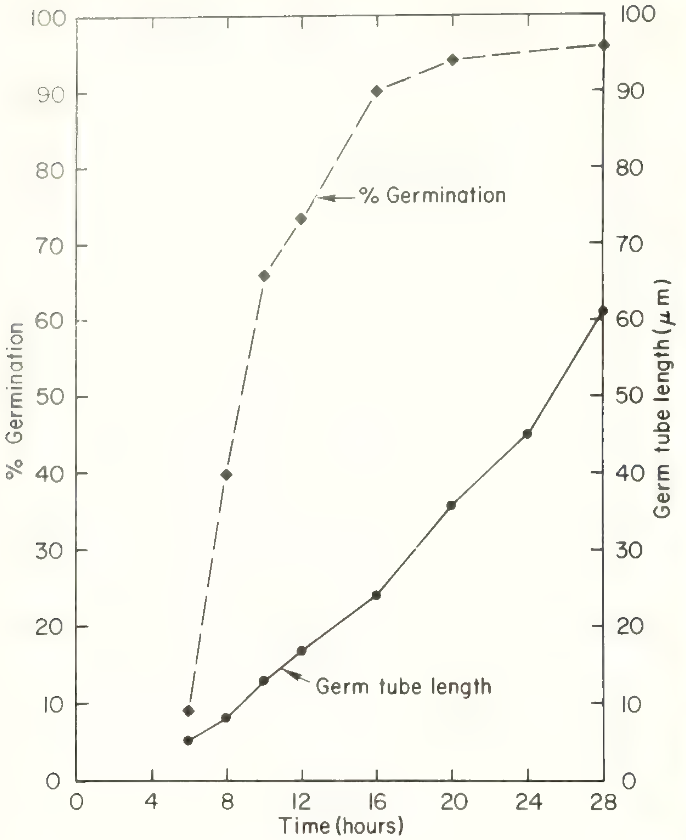

Figure 7-10.—Germ tube length and percent germination of *Cercospora sequoiae* var. *juniperi* spores incubated for various periods of time, at 24°C, on water agar.

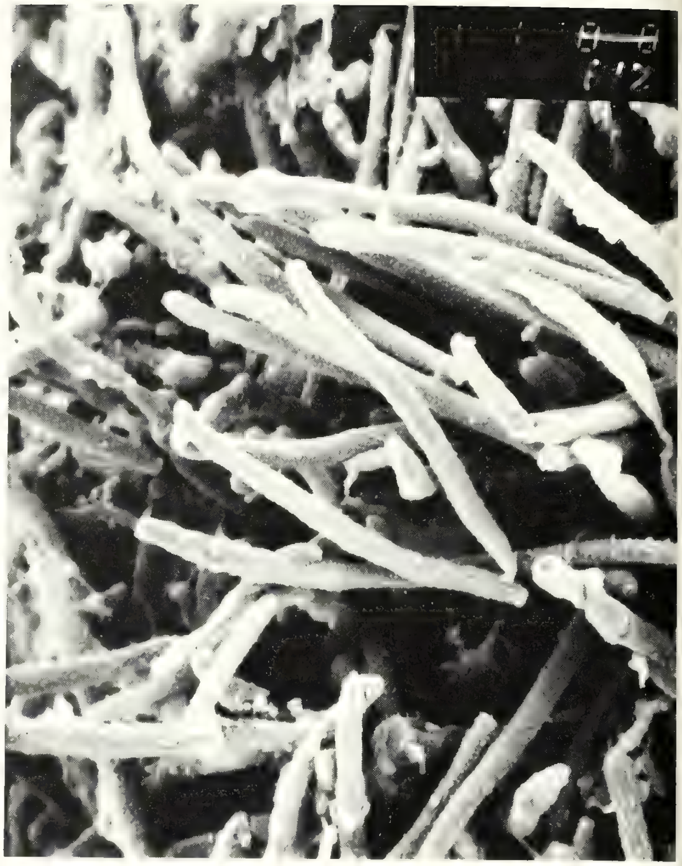

Figure 7-12.—Spiny surface of spores of *Cercospora sequoiae* var. *juniperi.* (X 3750)

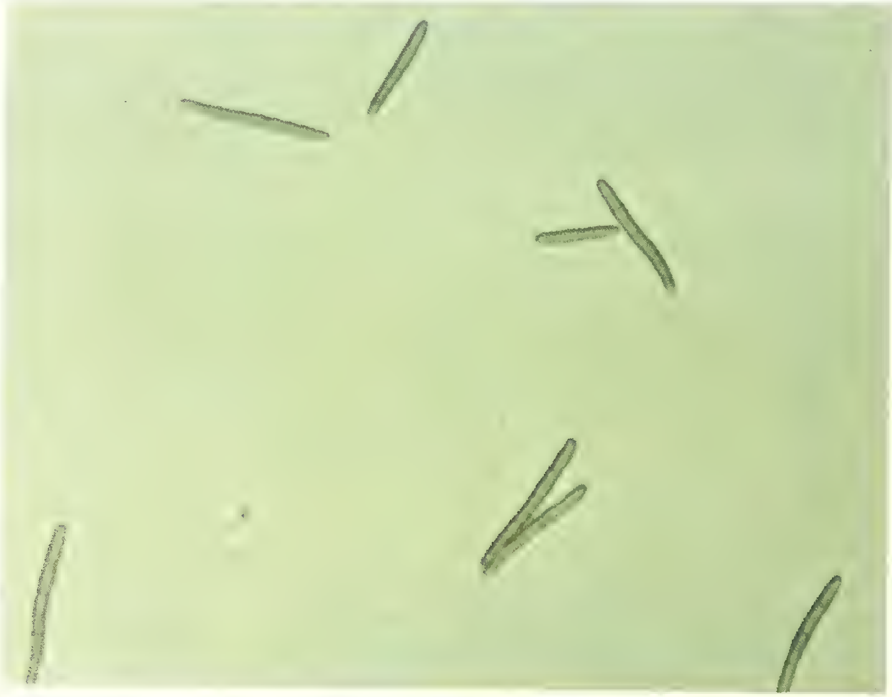

Figure 7-11.—Spores of *Cercospora sequoiae* var. *juniperi* showing cross walls (septations).

8. Kabatina Blight of Junipers

For several years, branch tips of eastern redcedar in Nebraska have been damaged by an unknown agent in plantings (fig. 8-1). Recently, the fungus *Kabatina uniperi* was found to be the cause of this damage. *uniperus scopulorum* is also infected.

There is very little information on the geographic distribution of this fungus in the Great Plains or in the rest of the United States; it has been found in Nebraska, Indiana, Wisconsin, and New Hampshire.

Diagnosis and Life Cycle

The symptoms of Kabatina blight are first evident in the spring at the time when juniper foliage turns deep green. Foliage on branch tips infected with *K. juniperi* turn yellow-brown instead of green (fig. 8-2).

The average length of dieback of diseased branches of eastern redcedar was 128 ± 50 mm. An average of 10 mm of this dieback was covered with *K. juniperi* fruiting bodies (acervuli). Average twig diameter at the base of the dieback was 1.6 ± 0.4 mm.

The fruiting bodies of *K. juniperi* are usually present at the base of discolored foliage in a zone of sunken tissue (fig. 8-3). The fruiting bodies are numerous in April and May, but decline in number throughout the summer. Hyaline, ellipsoid, one-celled spores (4.5-8.0 μm by 2.3-3.0 μm) are formed singly at the tips of septate sporophores (fig. 8-4).

The damage caused by *K. juniperi* resembles damage caused by *Phomopsis juniperovora* (compare figs. 8-1 and 6-11). The time of symptom development is helpful in distinguishing these two blights. Kabatina blight symptoms develop before new growth begins in the spring, whereas Phomopsis blight symptoms develop anytime during the growing season.

The period of infection is unknown. Tissues that become discolored in early spring probably are infected the previous year, because there are few spores available for infection at time of discoloration, and the weather conditions at time of discoloration probably would be unfavorable for infection.

Artificial inoculation of eastern redcedar seedlings revealed that only seedlings with wounded foliage became infected. Scanning electron microscope photographs revealed that the fungus grew profusely around wounds and entered leaves through wounds.

The cause of the wounds observed on foliage of eastern redcedar in eastern Nebraska plantings is unknown. However, two unidentified insects, capable of wounding foliage, have been found in eastern redcedar plantings infected with *K. juniperi*.

Control

No tests for control of this fungus have been conducted. Control tests are planned which will include both fungicides and insecticides, applied alone and in combination, at different times. The tests will be arranged so that the time or times when infection occurs can be determined.

Physiology and Morphology

The optimum temperature for growth of *K. juniperi* is 24°C (fig. 8-5). The optimum temperature for germination of spores of *K. juniperi* on water agar is 24°C; this temperature is also optimum for germ tube growth (fig. 8-6).

Germination began between 8 and 12 hours when spores were incubated on water agar at 24°C; about 80% of the spores had germinated with 20 hours of incubation (fig. 8-7).

Artifically inoculated eastern redcedar seedlings, incubated for 5 days, at 100% relative humidity, at 16°, 20°, 24°, or 28°C, became infected if foliage had been wounded before inoculation. Wounded, inoculated seedlings incubated for 24 hours, at 100% relative humidity, at 24°C, also became infected.

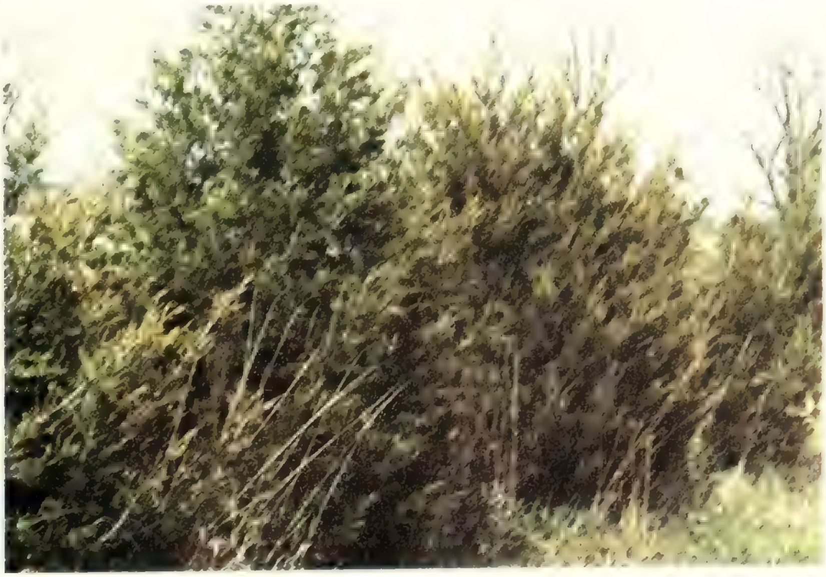

Figure 8-1.—Eastern redcedar damaged by *Kabatina juniperi*.

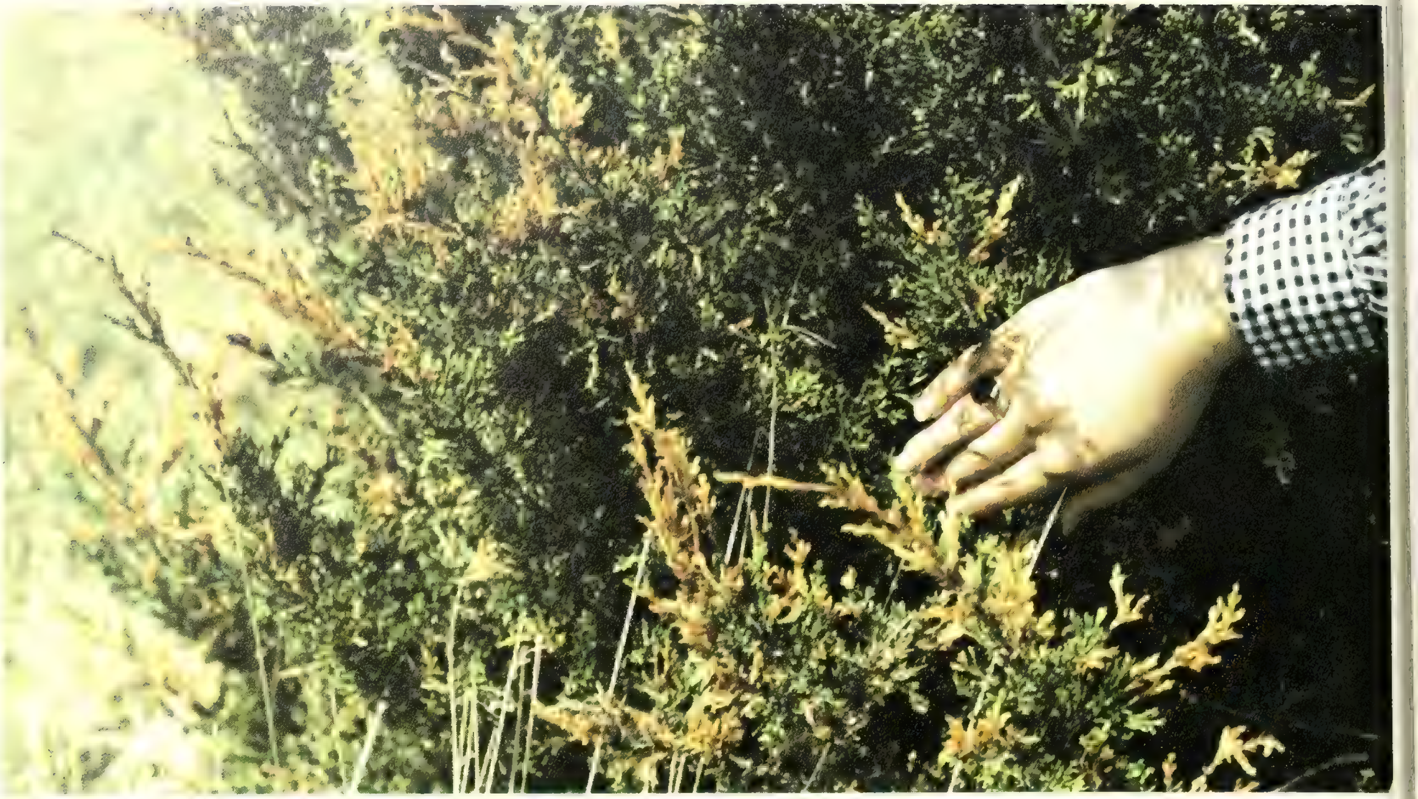

Figure 8-2.—Tips of eastern redcedar branches killed by *Kabatina juniperi.*

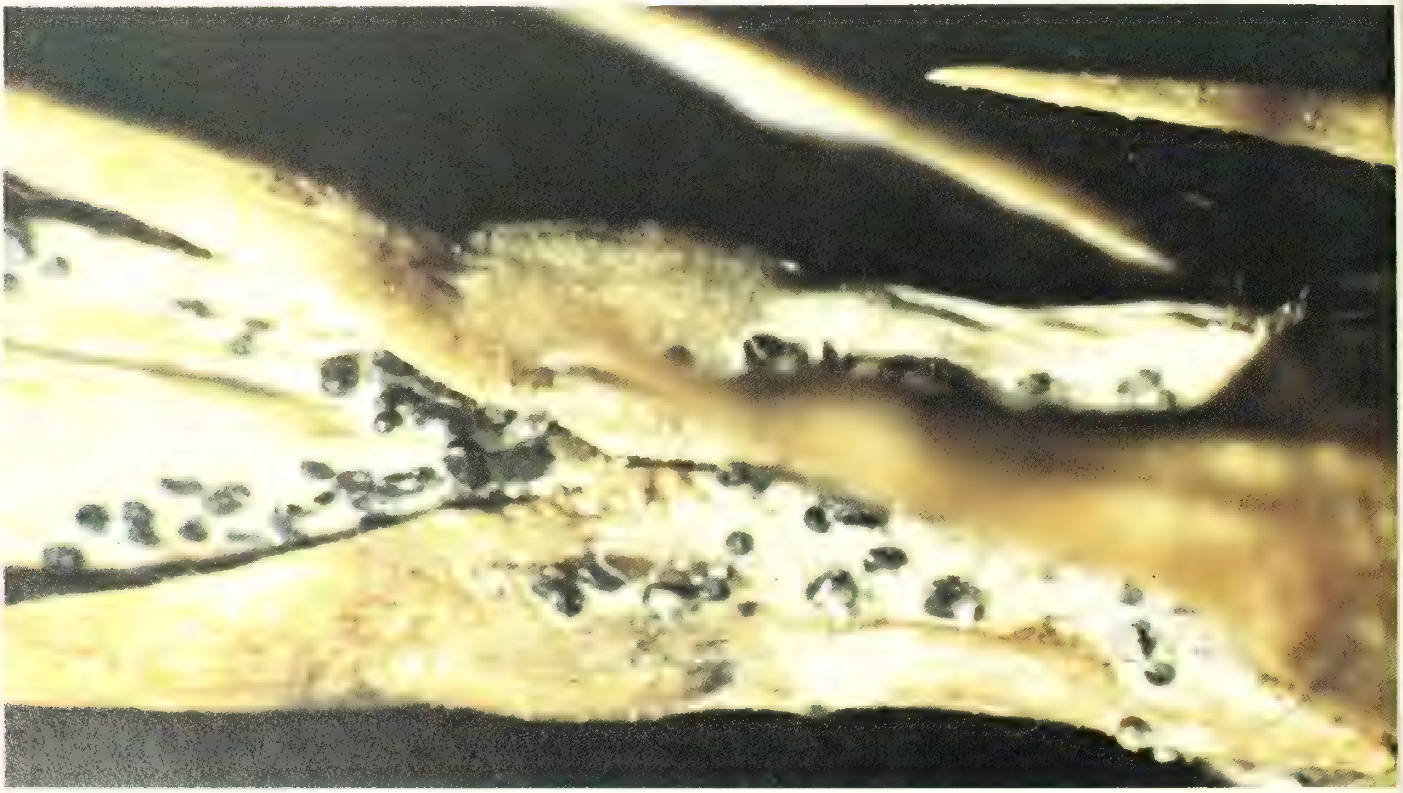

Figure 8-3.—Fruiting bodies of *Kabatina juniperi* on eastern redcedar.

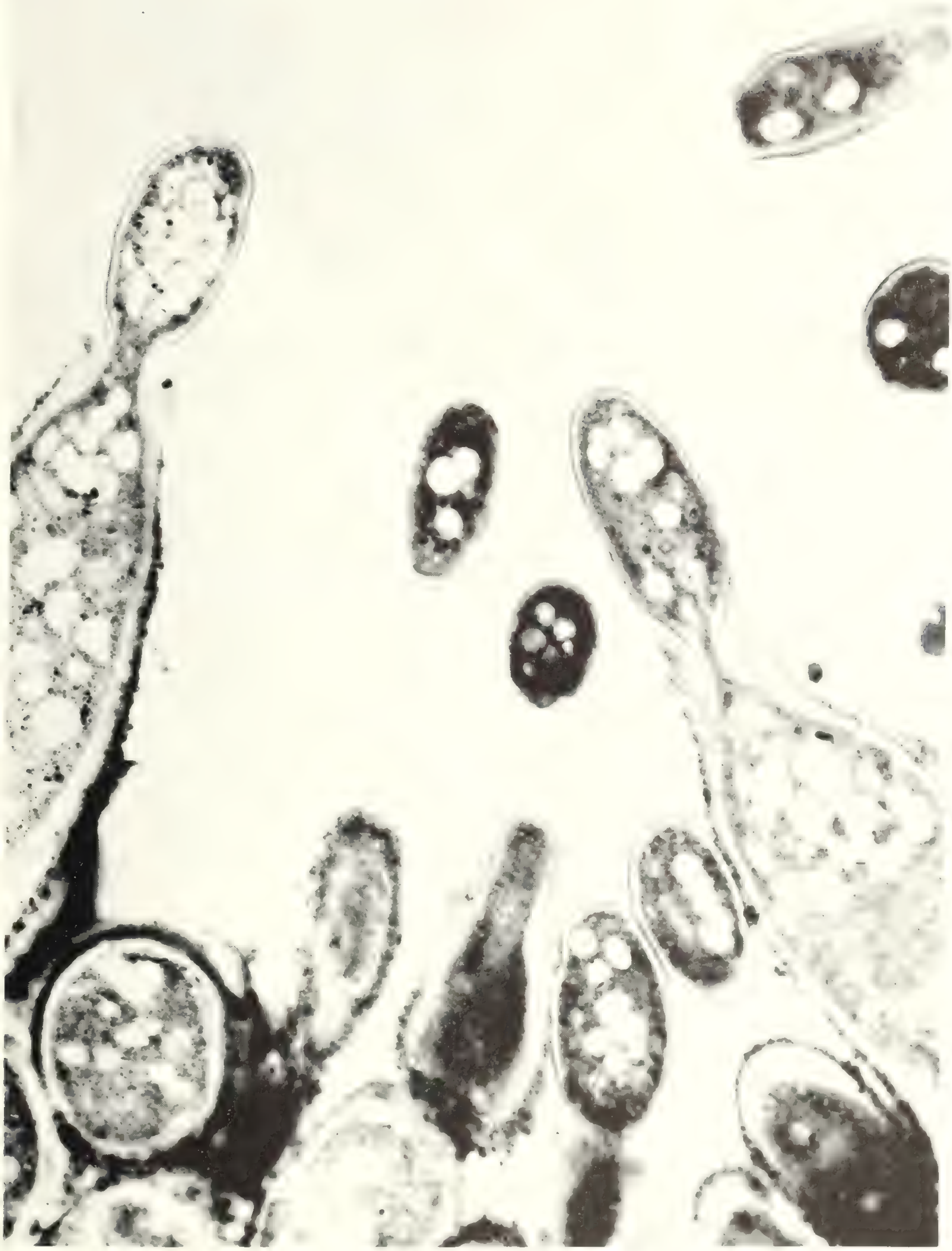

Figure 8-4.—Spores and sporogenous cells of fruiting body of *Kabatina juniperi*. (X 10,000)

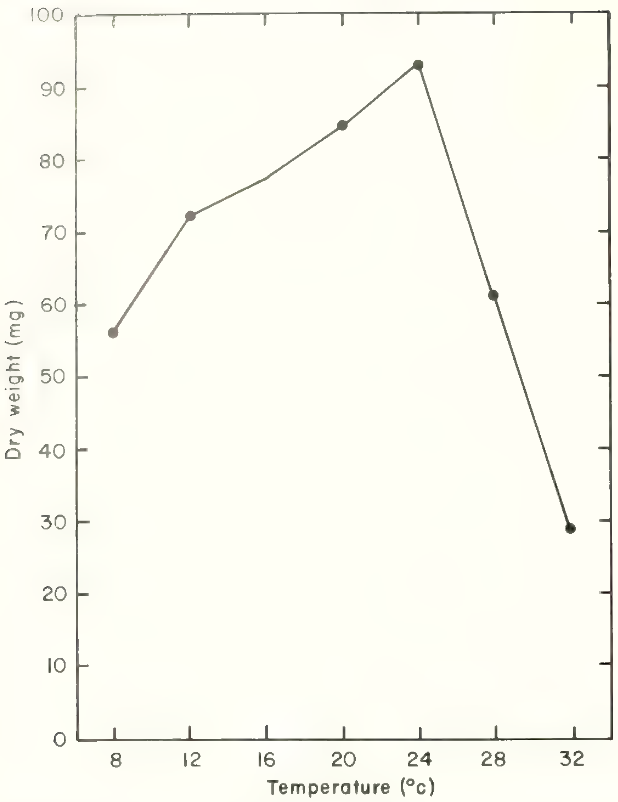

Figure 8-5.—Effect of temperature on growth of *Kabatina juniperi* in a liquid culture medium, after 7 days.

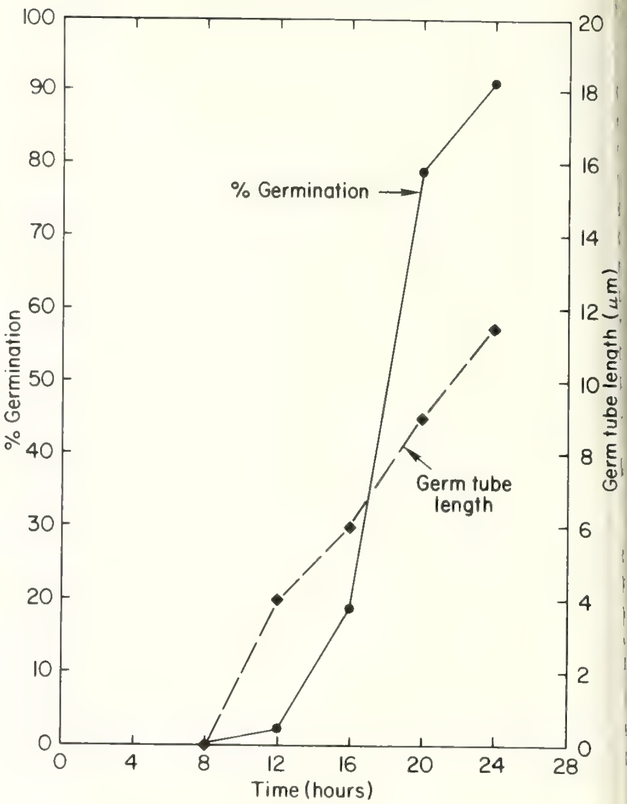

Figure 8-7.—Germ tube length and percent germination of *Kabatina juniperi* spores incubated for various periods of time, on water agar, at 24°C.

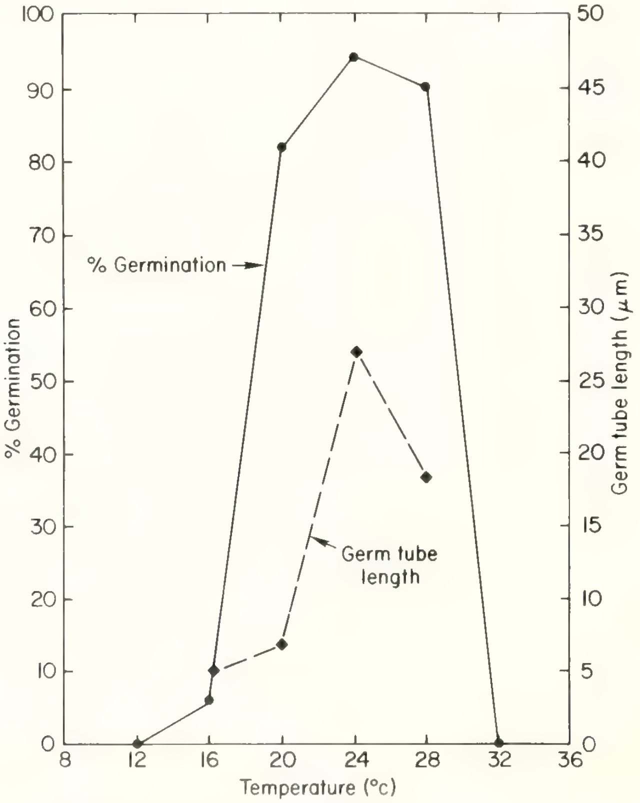

Figure 8-6.—Effect of temperature on germination of *Kabatina juniperi* spores incubated for 24 hours on water agar.

. Root Lesion Nematode Damage to Junipers and Pines

Nematodes infecting tree roots can cause large conomic losses in tree nurseries. The losses occur ecause the growth of seedlings is reduced to the extent that they are not salable. In addition, most states rohibit the sale of nematode-infected trees. The root esion nematode *Pratylenchus penetrans* has a very wide host range which includes many of the plant pecies commonly used for cover crops in tree nurseries. In the early 1960's, tree nurseries in the Great Plains were surveyed for damage by nematodes. Root lesion nematodes were encountered more frequently than other kinds of plant pathogenic nematodes.

Diagnosis and Life Cycle

Damage by root lesion nematodes was particularly severe in a forest tree nursery in north-central Nebraska. Eastern redcedar seedlings in beds adjacent to eastern redcedar windbreaks were in low vigor (fig. 9-1). There was no obvious damage to the aerial parts of junipers in the windbreaks. However, an examination of roots of the windbreak trees and roots of the adjacent seedlings revealed that they were infected with the root lesion nematode *P. penetrans*.

Before root lesion nematodes were found, several of the windbreaks had been removed because the nursery beds were being reoriented. The soil mounded in the windbreaks was spread out so that the nursery blocks would be relatively level.

Subsequently, eastern redcedar and Rocky Mountain juniper seeds were sown in the areas where windbreaks had been removed. At that time, seedlings were kept in beds for 2 years then transplanted for an additional year's growth before being distributed for field planting. Towards the end of the first growing season, there were some areas where seedling growth was much reduced. By the end of the second growing season the seedlings in these areas were stunted and in low vigor (fig. 9-2).

In every case, the low vigor seedlings had high infestations of root lesion nematodes. Root lesion nematodes are endoparasites—they enter roots and feed within them. As a consequence, many of the roots die, which accounts for stunted and low vigor seedlings. The seedlings whose roots were being killed formed new roots, which also became infected by the nematodes. These new roots were much larger and fleshier than normal roots. In checking for presence of root lesion nematodes, it was easier to use the fleshy roots because there were fewer kinds of nematodes than in the older roots.

Initially, damage was observed only on juniper roots. However, a check of roots of other seedlings revealed that all conifers growing in the nursery were hosts for this nematode. These trees were Austrian pine, ponderosa pine, jack pine, Colorado blue spruce, Black Hills spruce, eastern redcedar, and Rocky Mountain juniper.

The nematode problem in this nursery was increased when seedlings from affected areas were transplanted; root lesions nematodes were introduced into the transplant area of the nursery, which previously had been free of root lesion nematodes.

Control

After nematodes were detected, several control experiments were conducted to determine the most effective soil fumigant. The fumigant needed had to be one that would move into and out of the soil rapidly. This was necessary because both seeding and transplanting were done in the spring. Furthermore, all space in the nursery was being utilized during the growing season.

For effective fumigation, soil temperatures need to be at least 13°C. Because temperatures remained low early in the season, there was little time between lifting of seedlings and either seeding or transplanting.

Tests showed that methyl bromide was effective, and moved into and out of the soil rapidly. Therefore, seeding or transplanting could be done soon after fumigation (figs. 9-3, 9-4).

Soon after nematodes became a problem, the nursery, in an effort to reduce costs, explored ways of eliminating transplanting. Two methods were tried: (1) growing seedlings in the same beds for 2 years but at lower densities and with higher soil fertility, and (2) growing seedlings in the same beds for 3 years.

Evaluations showed that seedlings grown in beds that had been fumigated with methyl bromide were essentially free of nematode damage after two growing seasons; but if they remained in the beds for 3 years, the root lesion nematode populations increased to the level where the third-year seedlings were severely damaged.

In the fall, areas free of seedlings were commonly sown to rye or oats to reduce soil movement by wind. Unfortunately, both rye and oats were hosts of *P. penetrans* (fig. 9-5). The nursery now uses cover crops that are not hosts of *P. penetrans*.

This nursery produces high quality stock, but only because they use soil fumigants to control root lesion nematodes. The wide host range of the nematode, plus the fact that, even with the most effective fumigant, the nematode populations increase to damaging levels after 2 years, dictates that soil fumigation must remain a standard practice in this nursery (fig. 9-6). Soil fumigation has the added benefits of controlling weeds and reducing losses caused by damping-off disease fungi.

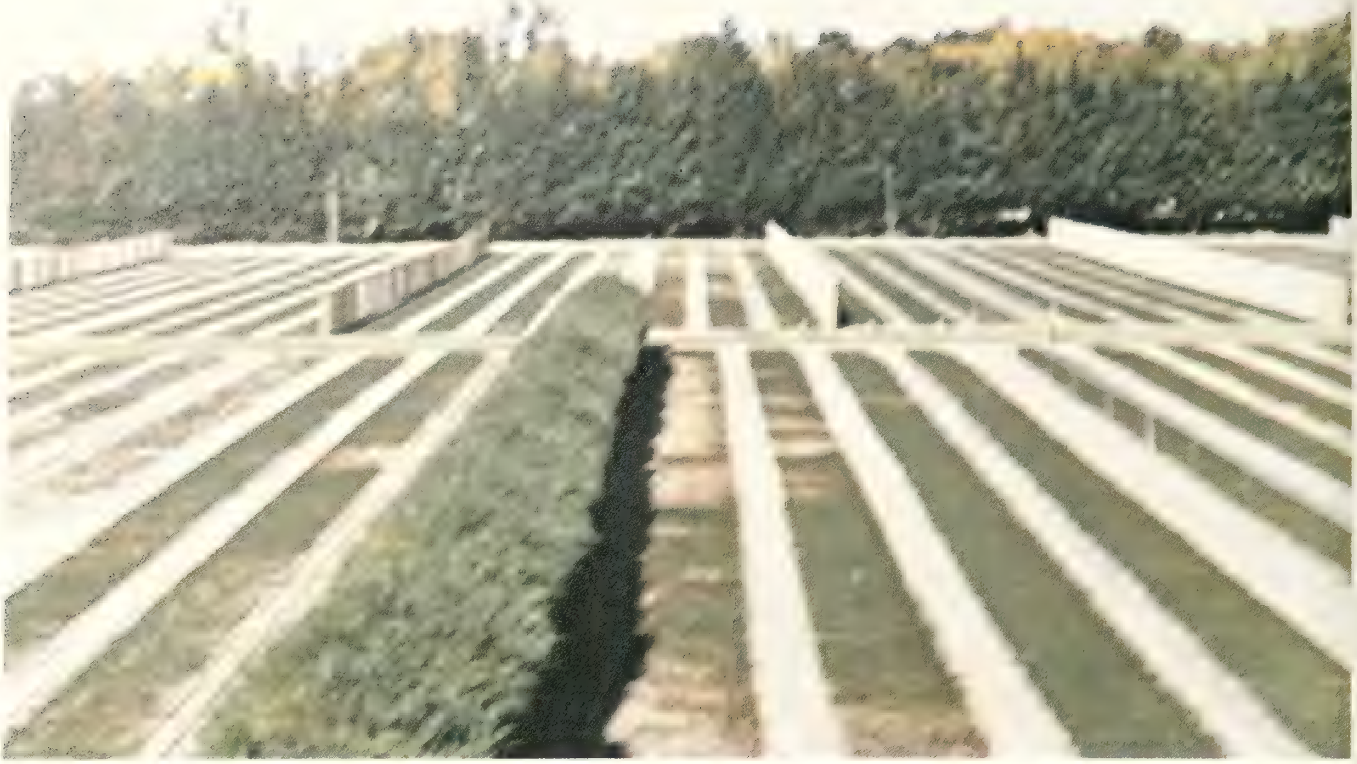

Figure 9-1.—Root lesion nematode damage to eastern redcedar seedlings, adjacent to an eastern redcedar windbreak that was heavily infected by root lesion nematodes.

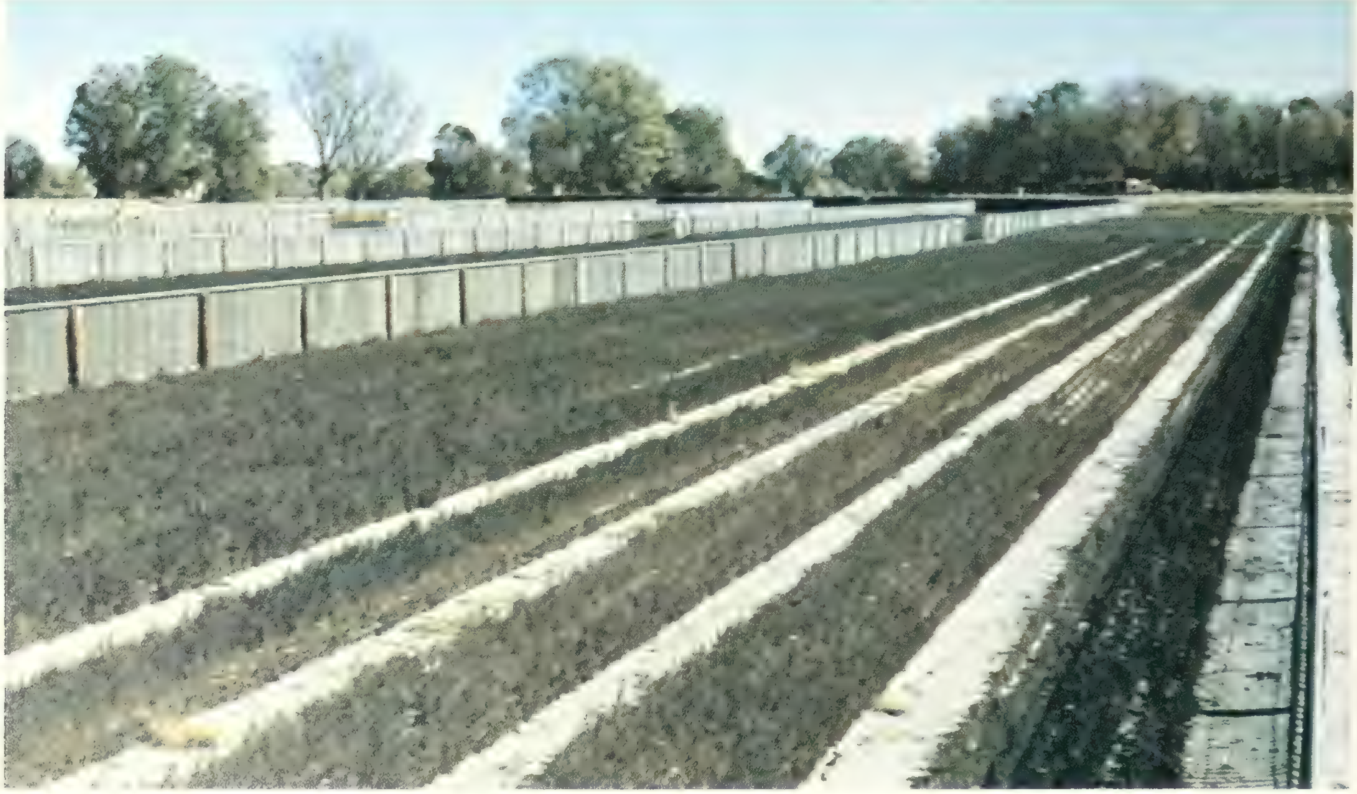

Figure 9-2.—Extensive root lesion nematode damage to eastern redcedar seedlings in an area where an eastern redcedar windbreak had been removed.

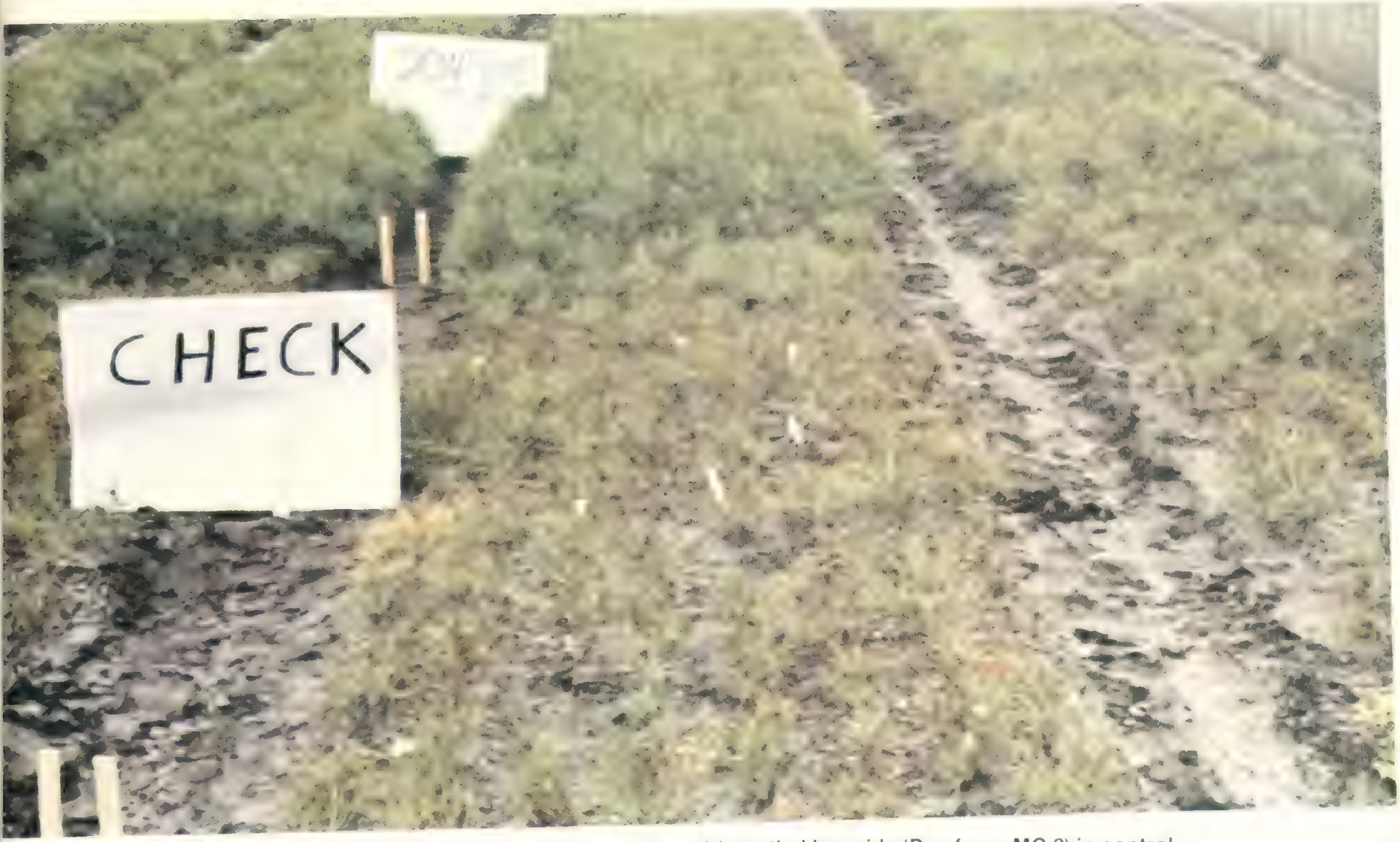

Figure 9-3.—Effectiveness of soil fumigation with methyl bromide (Dowfume MC-2) in controlling root lesion nematodes.

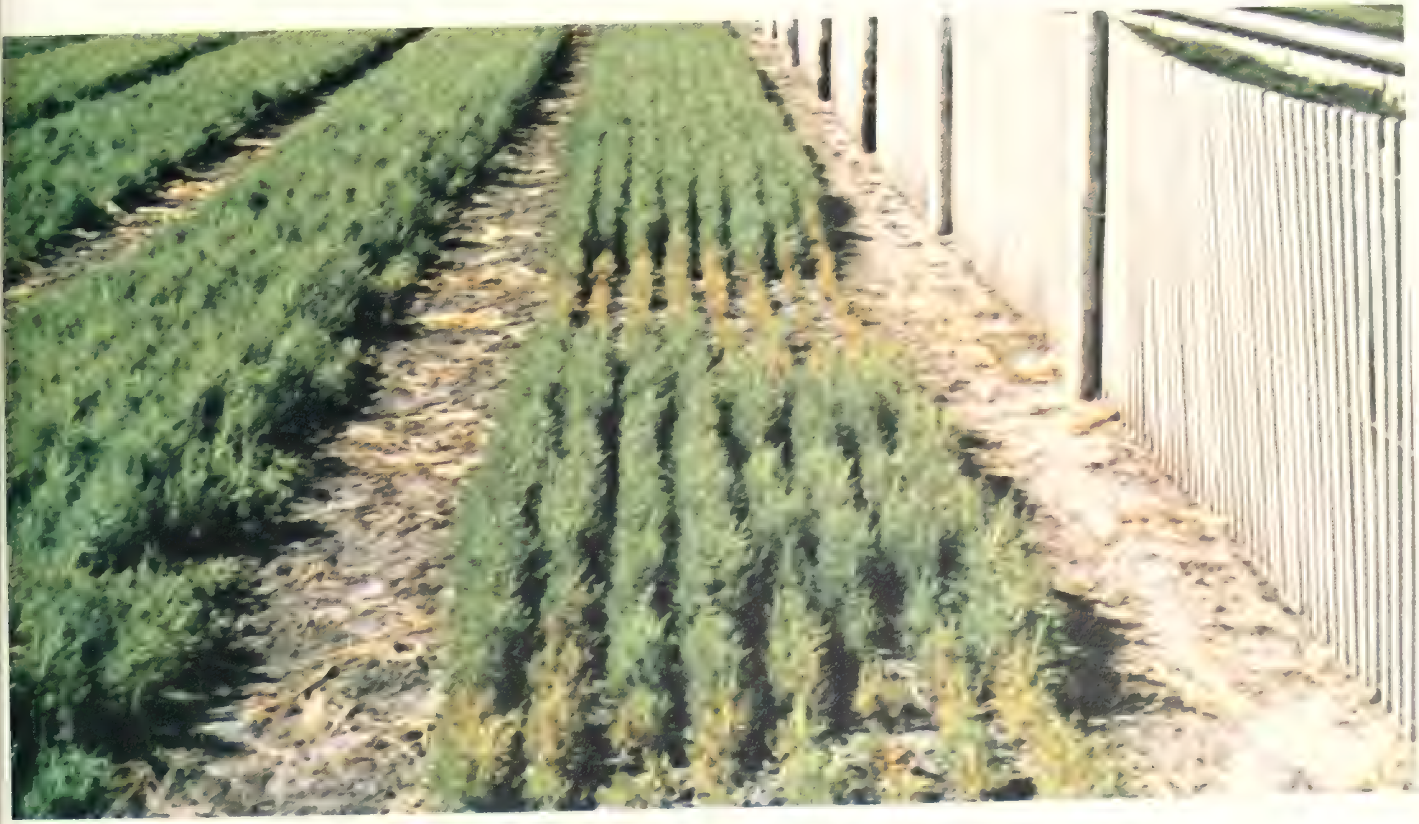

Figure 9-4.—Root lesion nematode (*Pratylenchus penetrans*) damage to eastern redcedar seedlings in a small area where soil was not fumigated with methyl bromide.

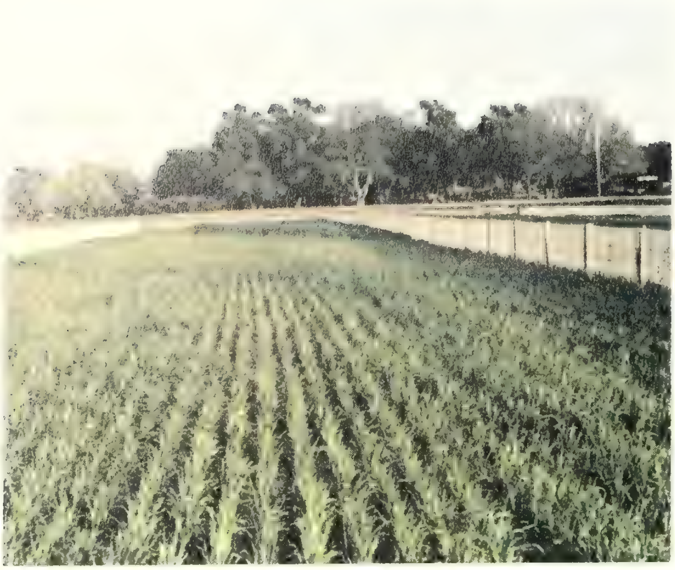

Figure 9-5.—A cover crop of oats severely damaged (foreground) by root lesion nematodes; tall, deep, green oats in background are not infected.

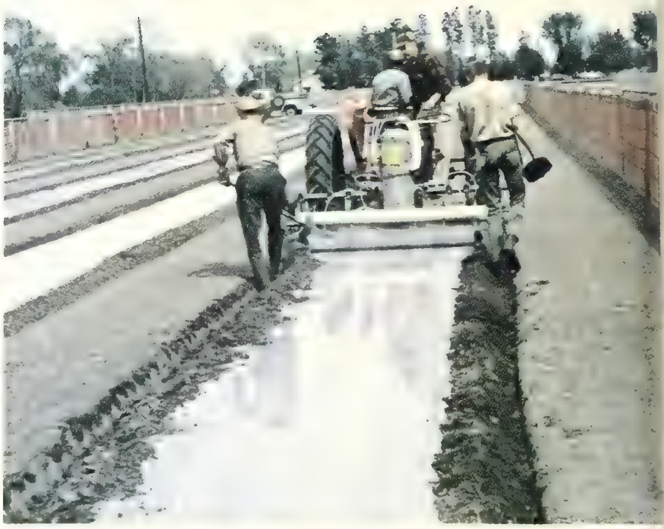

Figure 9-6.—Fumigation of nursery beds with methyl bromide t control root lesion nematodes.

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The results of research in the Great Plains on five diseases of pines (Dothistroma needle blight, brown spot disease, Diplodia tip blight, Naemacyclus needle cast, western gall rust) and three diseases of junipers (Phomopsis blight, Cercospora blight, Kabatina branch tip dieback) are presented.

Keywords: **Pinus, Juniperus,** tree diseases, Great Plains

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The Use of Multivariate Statistics n Studies of Wildlife Habitat

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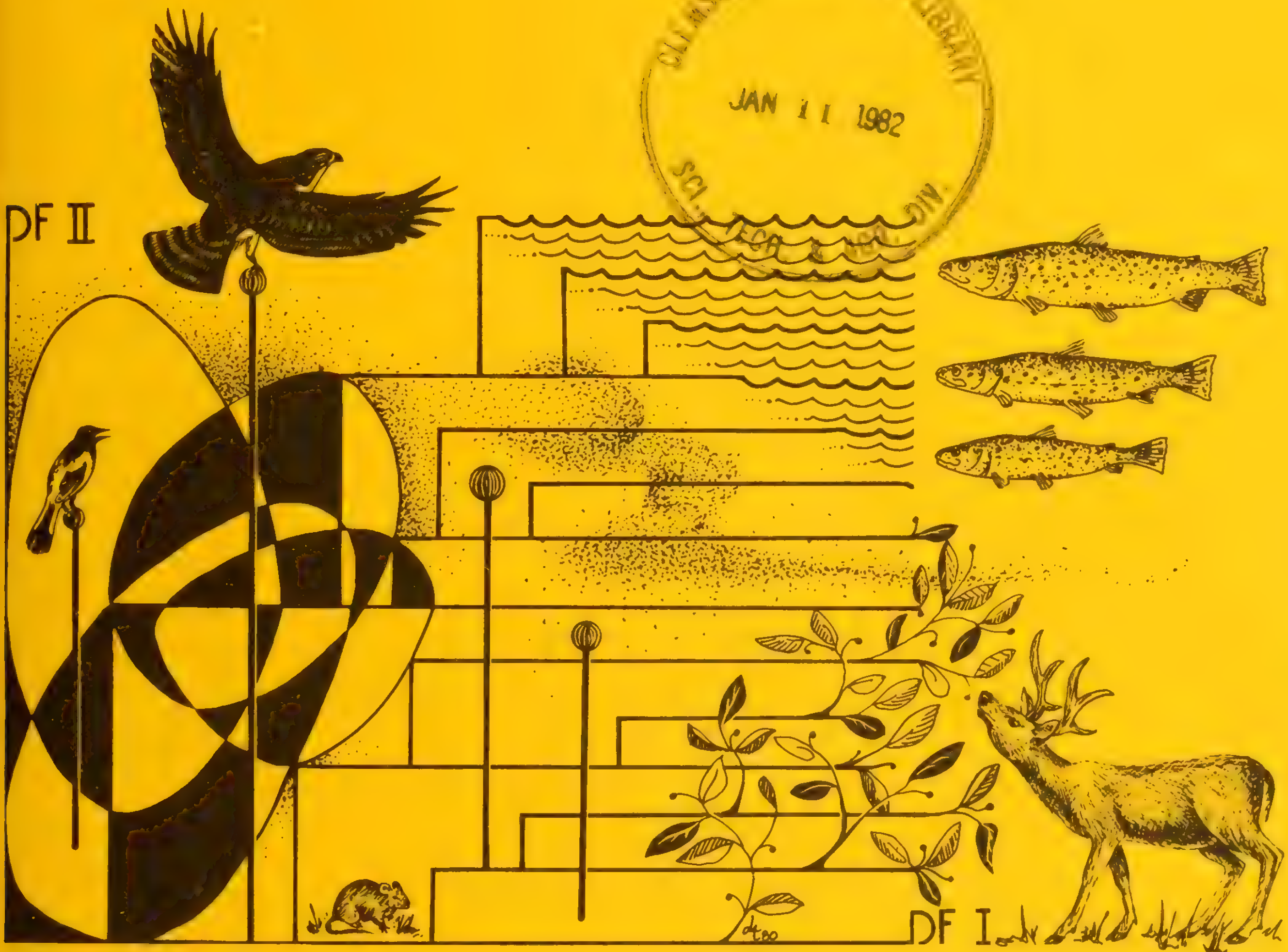

General Technical Report RM-87
Rocky Mountain Forest and
Range Experiment Station
Forest Service
U.S. Department of Agriculture

ABSTRACT

This report contains edited and reviewed versions of papers presented at a workshop held at the University of Vermont in April 1980. Topics include sampling avian habitats, multivariate methods, applications, examples, and new approaches to analysis and interpretation.

Limited numbers of reprints are available from the authors of each paper contained in this report.

USDA Forest Service
General Technical Report RM-87

August 1981

The Use of Multivariate Statistics in Studies of Wildlife Habitat[1]

Edited by

David E. Capen
University of Vermont

The workshop at which the papers included in this report were presented was jointly sponsored by

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The following session chairmen evaluated submitted abstracts and reviewed manuscripts: James Karr, University of Illinois; Barry Noon, U.S. Fish and Wildlife Service; Robert Whitmore, West Virginia University; Jake Rice, Arizona State University and Memorial University of Newfoundland; Mark Boyce, University of Wyoming, and Ray Dueser, University of Virginia.

Graduate assistants and research technicians, Allen Boynton, Douglas Inkley, Stephen Parren, Bill Roberts, Douglas Runde, Mark Scott, Diane Tessaglia, and Frank Thompson contributed greatly to the organization of the workshop.

Trish McLaren, Lisa Klein, and Richard Lent provided editorial assistance. Richard Lindeborg rendered valuable service as the editorial liaison with the Forest Service.

Diane Tessaglia designed and contributed the cover artwork.

Maureen Douglas put all the manuscripts and revisions on the word processor and produced the camera copy.

PREFACE

The commonly recognized multidimensional nature of wildlife habitat has led to a rapidly increasing use of multivariate statistical techniques in studies of wildlife ecology. Techniques such as discriminant function analysis, principal component analysis, factor analysis, and canonical correlation have been applied in studies of habitat selection and resource partitioning, ordination of habitats and simulation of habitat change, and in development of habitat inventory systems. Although multivariate methods are not understood easily, they may be employed with little difficulty if one has access to a computer. Such convenience tempts researchers to employ sophisticated analytical techniques but overlook important statistical assumptions, experimental design, and biological interpretation. With these temptations in mind, a meeting was organized to bring research biologists and statisticians together to discuss multivariate methods and their applications to studies of wildlife habitat.

The meeting (held at the University of Vermont, Burlington, April 23-25, 1980) was called a workshop, although it was not unlike a research symposium. It was a working conference and participants took an active role in discussing and critiquing topics of concern. Biologists learned from statisticians and vice-versa. Interactive sessions and productive interchanges of ideas satisfied the workshop's purpose of encouraging the use of improved statistical methods in studies of wildlife habitat and fostering better interpretation of research results. It is hoped that these published proceedings will encourage other investigators to improve design of their research, analyses of their data, and interpretation of their results.

The papers presented at the workshop were either invited or submitted by abstract. Those papers are the basis of this report. Following the workshop, authors revised manuscripts and incorporated discussion from the meeting. Additional comments and critiques were recorded, edited, and added to papers where appropriate. Manuscripts were subsequently reviewed and revised so that these proceedings could be drawn together to form a cohesive volume, rather than a mere collection of papers.

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SUMMARY OF THE WORKSHOP[1]

Stanley H. Anderson[2] and David E. Capen[3]

BACKGROUND

Wildlife habitat evaluation studies have progressed from purely descriptive work involving a discussion of community types and plant species present through concepts of vegetation function, physical structure, and vegetation structure. Many forms of special habitat descriptors, such as life forms or physiognomy, have been used.

Recently, resource agencies have been looking at means of evaluating wildlife habitat with ideas of describing changes that occur in wildlife populations as a result of habitat alteration. Five federal agencies (Forest Service, Fish and Wildlife Service, Soil Conservation Service, Geological Survey, and Bureau of Land Management) are working out a joint agreement for gathering and classifying wildlife habitat on a regional basis. Some federal agencies, many states, and some private organizations are developing data systems that include large amounts of wildlife habitat data. Objectives of these systems are to quickly classify wildlife habitat and indicate what changes might occur in wildlife as a result of widespread changes in the environment. Obviously, the utility of these systems depends on the type of data they contain.

Most papers presented at the workshop and included in these proceedings relate to species and groups of species. The application of wildlife habitat evaluation techniques has, therefore, jumped ahead of standardization of methods and development of analysis techniques. Development was the primary point of discussion in the workshop.

The computer age has revolutionized the analysis of research data. Statistical techniques are easily available to assist the biologist in examining relationships between wildlife and wildlife habitat. Techniques only theories two decades ago, are now employed routinely through the use of "canned" computer programs. Users of multivariate statistical methods requiring matrix algebra must rely on computers to analyze very large sets of data. Unfortunately, computer programs do not have control over either the quality of data analyzed or interpretation of results. Also, the researcher may have little knowledge of the proper type of program or method to be used for different forms of data. Yet multivariate analyses are becoming standard procedure in ecological studies.

CONTENT

Overview and Cautions

H.H. Shugart keynoted this meeting by pointing out that multivariate statistical techniques as methods of choice in analyzing habitat data among animals have three distinct advantages over alternative methodologies: 1) multivariate procedures intrinsically fit ecological problems (and data) of this sort; 2) many multivariate methods seem to be robust in the face of mild deviations from underlying assumptions; and 3) there already exists a hypergeometric interpretation of the relationship among animals (niche theory) that is essentially based on a multivariate sample space. He also discussed the need for more information on density, which has not been emphasized in most multivariate studies. His opening remarks initiated a recurring theme that biologists have not always planned statistical analysis prior to collecting data. Rather, they have sought statistical advice after massive amounts of data were gathered.

Douglas Johnson, an experienced biometrician, initially was invited to respond in a general sense to papers presented at the meeting. His response evolved into a comprehensive review of essential considerations which should preceed multivariate analyses; considerations such as non-linear response functions of wildife species to their habitats. This paper should be read before wildlife habitat studies are designed, and before multivariate methods are even selected to explore relationships or confirm hypotheses.

---

[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-35, 1980, Burlington, Vt.

[2] Leader, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071.

[3] Assistant Professor, Wildlife Biology Program, University of Vermont, Burlington, VT 05401.

A more dramatic cautionary presentation was made by James Karr and Thomas Martin. These authors describe a study of bird/habitat relationships where habitat variables were reduced to "meaningful" axes by principal components analysis (PCA). Surprisingly, their habitat data were collected from a random numbers table, but findings compared favorably with those from published reports of real--we assume--bird/habitat studies. This paper emphasizes the importance of objective interpretation of PCA.

Habitat Measurements

A satellite session presented the opportuntiy to back away from data analysis and focus on habitats *per se*. This session, although restricted to avian habitats, provided both a theoretical and practical framework for designing studies of wildlife habitat relationships. The six speakers presented first a historical review of why we measure habitat and a theoretical perspective of how birds use multidimensional resources. Then there were discussions of how to select the proper habitat variables; how to measure them; and how to design statistical treatment for the data. Statisticians with little knowledge of biological processes will appreciate this chapter of the proceedings.

Theory and Methods

Biologists must have an understanding of multivariate statistical theory and methodology before employing these techniques in research endeavors. Papers given by Williams, Bhattacharrya, and Smith addressed the more commonly used methods employed in ecological studies. Ken Williams discussed problems in using discriminant function analysis (DA) in terms of habitat variables approching normality, problems of covariance equality in canonical analysis, and possible statistical violations found in the literature that have resulted in misinterpretation of data. His paper is of particular consequence in satisfying objectives of the workshop and the proceedings. Following Williams' presentation of the structure of canonical variates, Kim Smith gave an extensive review of the uses of canonical correlation in ecological work and formulated some important recommendations for improved use of this technique in our discipline. Research biologists are directed, in particular, to Smith's recommendations on sample size. Helen Bhattacharrya's presentation was an easily understood explanation of principal component analysis and its many variations. James Dunn prepared a particularly comprehensive treatment of transformations for univariate and multivariate data; this paper emphasizes the need for a thorough understanding of statistics before taking advantage of the more advanced options available in this area of quantitative science.

Application

Fourteen speakers gave papers which illustrated how multivariate techniques have been applied to field studies of a variety of different organisms. Andrew Carey uses PCA of a montane ecosystem to illustrate a suggested terminology for such ecological work. On a more applied basis, Tom Smith and co-authors Shugart and West show how important elements of a forest habitat can be identified by DA and incorporated into simulation models which predict habitat availability for selected species of birds. Chris Grue and co-investigators Reid and Silvy used stepwise multiple regression and DA to condense a large number of habitat variables into workable models for a large-scale classification and inventory system. Workshop participant Paul Geissler critiqued their study design by emphasizing the potential for prediction bias when the number of variables exceeds sample size. Like Karr and Martin, Geissler used a random number universe to illustrate his point.

Six of these 14 examples of multivariate applications may be studied as a collection of contrasting approaches to a variety of ecological problems. Martin Raphael used DA and cluster analysis to study nesting habitat of sympatric cavity-nesting birds. Mark Boyce and Joe Folse used canonical correlation in their studies of bird habitats. Boyce describes a robust analysis of sage grouse habitat, while Folse employs canonical correlation as an ordination technique, an unusual application. Brian Maurer and co-authors McArthur and Whitmore used PCA in what has become a common format in bird/habitat studies, but introduced a procedure of obtaining weighted mean values for habitat variables. Phil Sczerzenie applied PCA and PC-regression to deer harvest-land use relationships and illustrated the use of these techniques on an expanded spatial scale. Tom Harshbarger and Helen Bhattacharrya contributed the only paper where multivariate techniques were used in a study of an aquatic species, trout. Their conclusion was that regression models based on derived factors were no better than models composed of original variables.

New Approaches

Five research papers were particularly relevant to the purposes of the workshop; these presentations introduced both new statistical applications to familiar problems and new field approaches to familiar statistics. Jake Rice, R.D. Ohmart and B.W. Anderson illustrated the importance of seasonal and annual variation when using DA to classify avian habitats. The application of their findings cannot be overlooked. John Rotenberry and John Wiens also used a familiar approach, PCA, but reported an innovative technique of combining species abundance and habitat relationships in the same environmental space.

The remaining papers dealt with the important topic of robust procedures. Jim Harner and R.C. Whitmore described new techniques which are robust to outlying data; their computer programs will be sought by many investigators. The problem of multicollinearity is addressed by Janet Cavallaro, J.W. Menke, and W.A. Willimas; their use of ridge regression to deal with this problem is applaudable. Multicollinearity is also highlighted in Kathryn Converse and B.J. Morzuch's paper.

Lyman McDonald, like Doug Johnson, is a statistician who has worked extensively with wildlife research problems. He too was asked to respond in general to papers presented at the workshop. Dr. McDonald reviewed papers and chose to concentrate on robust procedures, indicating the importance of this topic to wildlife habitat studies. His comments are found after those papers which address robust techniques.

CONCLUSION

Although insights often occur when techniques do not work, we must adhere to basic scientific premises. Multivariate analyses are useful tools for describing wildlife habitat only when properly applied; when misused or abused they become not only ineffective, but also disastrously misleading. It is important to remember that multivariate statistics alone do not solve problems; they only assist us in using our knowledge to interpret large amounts of data. We should not try to make sense out of nonsense; however, exploratory studies are valid when they follow the stated purpose.

To competently continue our work in examining wildlife habitat, it is most important for us to clearly define the problem at the outset of each study. This means setting objectives, establishing hypotheses that can be tested, and determining the forms of data to be collected and how they should be analyzed statistically. These steps will help determine data collection procedures. At this point it is extremely important to know the assumptions of tests to be used and make sure that these assumptions are met in the data collection procedure. Finally, we must recognize that results of the tests are not an end in themselves, they only provide direction. We must return to the field and validate the results, frequently through manipulative experiments. We as investigators, teachers, and scientific reviewers, must encourage proper interpretation through our selection of tests.

Site-specific studies must be used as one example of regional and national application. Researchers must be keenly aware of their need to design experiments and translate results into meaningful information for teachers, managers, and lawmakers. A cautionary question: are we publishing our results too soon? Maybe studies should go beyond the typical one or two years and proper verification should follow.

We hope this symposium of biologists and mathematicians is of help to all involved. The demands for the information we gather are great but it is important that we pass on only the best information. The type of interaction brought about by this workshop needs to continue.

AN OVERVIEW OF MULTIVARIATE METHODS AND THEIR APPLICATION TO STUDIES OF WILDLIFE HABITAT[1]

H.H. Shugart, Jr.[2]

Abstract.--Multivariate statistical techniques as methods of choice in analyzing habitat relations among animals have three distinct advantages over competitive methodologies: 1) Multivariate procedures intrinsically fit ecological problems (and data) dealing with habitat selection. 2) Many of the multivariate methods seem to be robust in the face of mild deviations from the underlying assumptions. 3) There already exists a hypergeometric interpretation of relations among animals (niche theory) that is essentially based on a multivariate sample space. These considerations, joined with a reduction in the cost of computer time, the increased availability of multivariate statistical "packages," and an increased willingness on the part of ecologists to use mathematics and statistics as tools, have created an exponentially increasing interest in multivariate statistical methods over the past decade. The earliest multivariate statistical analyses in ecology did more than introduce a set of appropriate and needed methodologies to ecology. These studies emphasized different spatial and organizational scales from those typically emphasized in habitat studies. The traditional wildlife habitat study was based on measuring the density of a population in a homogeneous plant community. New studies, using multivariate methods, emphasized individual organisms' responses in a heterogeneous environment. This philosophical (and to some degree, methodological) emphasis on heterogeneity has led to a potential to predict the consequences of disturbances and management on wildlife habitat. One recent development in this regard has been the coupling of forest succession simulators with multivariate analysis of habitat to predict habitat availability under different timber management procedures.

Key words: Habitat selection; multivariate statistics, quantitative ecology; succession models; wildlife-vegetation interactions.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

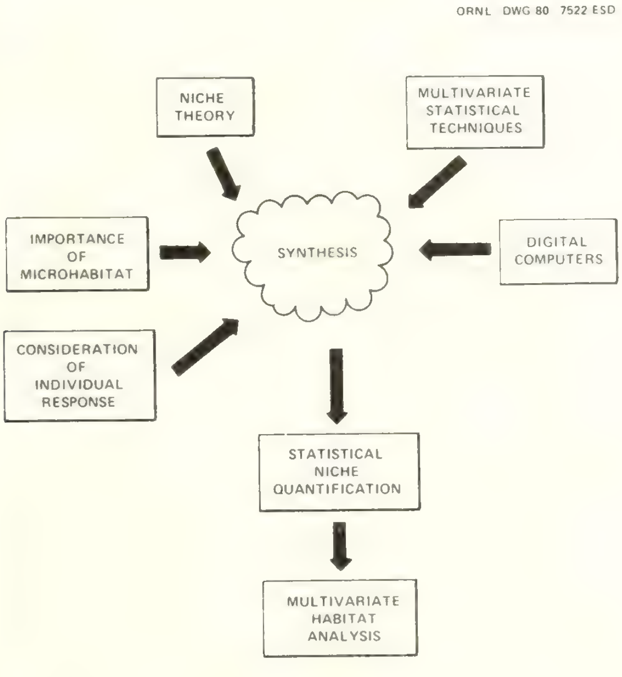
[2] Senior Research Staff Member, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830.

INTRODUCTION:

THE EVOLUTION OF MULTIVARIATE HABITAT ANALYSIS

Investigators in research centers all over the world, and particularly in the United States, are discovering applications of multivariate statistical techniques in studying the habitat relations of a diverse range of animals and plants. Given the suitability of multivariate statistics for habitat analysis coupled with the need for a wider understanding of animal/environment relations mandated by man's increasd use of the earth's resources, this is a logical situation. Indeed, the logic of using multivariate analysis to manage animal habitat would seem to make such applications inevitable. Yet only a decade ago, no studies that are methodologically and philosophically equivalent to those of today were in evidence. This paper takes as its central tenet that multivariate statistical analysis of habitat requirements of animals is the product of a synthesis, occurring in the early 1970's at several different research centers, that united different lines of scientific research.

Figure 1 illustrates the main elements of this synthesis. Two developments that were independent of ecological studies, the increased availability of computer time on high-speed digital computers and the development of multivariate statistical techniques, were combined with three ecological developments: 1) the hyperspace theory of the niche, 2) the realization that small spatial-scale studies could reveal much on animal interrelations, and 3) an emphasis on individual organism response as being important in determining species distributions. A number of papers developed various aspects of what was to become multivariate analysis published before the 1970's, but most of these papers did not combine all elements of the synthesis (table 1). MacArthur's (1958) classic work emphasized a relation between individual microhabitat utilization and the hyperspace niche theory model (Hutchinson 1944, 1957, 1965). Klopfer (1965) developed an impressive line of research in associating individual organism responses to microhabitat, as did Wiens (1969). Cody (1968) and Fujii (1969) both developed the idea of using multivariate statistics in studies of animal niches. In 1971 and 1972 a number of papers, by individuals working independently, appeared that combined these elements and attempted to quantify niches of various organisms (Green 1971, Hespenheide 1971, James 1971, Martinka 1972, Shugart and Patten 1972). The management implications of these works became obvious to various individuals and within a few years several papers had appeared that discussed the use of multivariate habitat analysis as a management tool. Because of its synthetic origins, multivariate habitat analysis can be considered in terms of the elements that formed this synthesis and in terms of the problems intrinsic to these synthesis elements.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NICHE THEORY
MULTIVARIATE STATISTICAL TECHNIQUES
IMPORTANCE OF MICROHABITAT
SYNTHESIS
DIGITAL COMPUTERS
CONSIDERATION OF INDIVIDUAL RESPONSE
STATISTICAL NICHE QUANTIFICATION
MULTIVARIATE HABITAT ANALYSIS

Figure 1. Schematic diagram of the scientific research elements that combined in a synthesis to produce multivariate habitat analysis.

ELEMENTS OF SYNTHESIS

Quantitative Elements: Statistics and Computers

Two of the most important elements that led to the development of multivariate habitat analysis were the state of development of multivariate statistical procedures and the increased availability of high-speed digital computers. It is interesting to note that current user-oriented statistical analysis procedures (e.g., Cooley and Lohnes 1971, Dixon 1974, Barr et al. 1976) are further accelerating the "computerization" of ecological studies in general. Many of the statistical procedures used in multivariate habitat selection studies require rather involved numerical analysis programs that: 1) use computers and 2) would be difficult for ecologists to develop de nova.

The availability of multivariate statistical analysis programs and computer time created a situation in which the initial work in developing habitat analysis techniques in the 1970's was often done in conjunction with a consulting statistician (e.g., Dr. J.E. Dunn, a contributor to these proceedings). This has had a positive effect in that the rigor in testing to meet statistical assumptions, in using the "right" methodologies, and in interpreting results correctly is much higher in multivariate habitat analysis than in botanical ordination and classification procedures. Ecologists interested in plant ordination developed a number of analytical techniques with little rigor relative

Table 1. Papers involved with animal/habitat relationships before and during the synthesis period for multivariate habitat analysis. A "yes" to Niche theory indictes the paper is strongly oriented toward niche theory; "yes" to Microhabitat indicates a use of a small spatial scale sample size; "yes" to Individuals indicates an emphasis on individual organisms; "yes" to Management indicates management potential is discussed in paper.

Multivariate paper	Taxa	Methods	Niche theory	Microhabitat	Individuals	Management
MacArthur (1958)	Birds	-	Yes	Yes	Yes	-
Klopfer (1965)	Birds	-	-	Yes	Yes	-
Wiens (1969)	Birds	-	-	Yes	Yes	-
Cody (1968)	Birds	Discriminant function (DF)	Yes	-	Yes	-
Fujii (1969)	Insects	Principal components analysis (PCA)	Yes	-	Yes	-
Green (1971)	Molluscs	DF	Yes	Yes	-	-
Hespenheide (1971)	Birds	DF	Yes	Yes	-	-
James (1971)	Birds	DF, PCA	Yes	Yes	Yes	-
Martinka (1972)	Birds	DF	Yes	-	-	Yes
Shugart and Patten (1972)	Birds	DF, other techniques	Yes	Yes	Yes	-
Anderson and Shugart (1974)	Birds	DF, PCA	Yes	Yes	Yes	Yes
Green (1974)	Benthic Animals	DF	Yes	Yes	Yes	-
Shugart et al. (1974)	Birds	DF, PCA	Yes	Yes	Yes	Yes
Shugart et al. (1975)	Birds Mammals	DF	Yes	Yes	Yes	Yes
Conner and Adkisson	Birds	DF	Yes	Yes	Yes	

to underlying statistical assumptions. The difference in rigor between plant ordination and animal habitat analysis is quite pronounced to anyone who has worked in both areas. While this would appear to be a positive attribute relative to habitat studies, this is not necessarily the case as I will discuss below.

Niche Theory

Hutchinson (1944, 1957, 1965) formulated a hypergeometric model of the niche of an organism that captured the imagination of theoretical ecologists for several decades (e.g., Horn 1966, Maguire 1967, McNaughton and Wolf 1970, Colwell and Futuyma 1971, Pielou 1972, May 1974, 1975), although this geometric interpretation has tended to be lost from more recent interpretations. The hypergeometric concept of the niche and the n-dimensional sample space are analogous in many respects, and this analogy was noticed by several early investigators (Table 1). The existence of a set of theories (niche theory) has led to an extended level of interpretation of multivariate habitat studies. Thus, one can interpret lack of overlap in terms of theories of "limiting similarity" or "competitive exclusion" (Harner and Whitmore 1977, Dueser and Shugart 1978). Further, the pattern of the means in a sample or discriminant space can be interpreted relative to theories of community structure (Shugart and Patten 1972, Dueser and Shugart 1979).

Consideration of Individual Responses and the Importance of Microhabitat

Population-level censuses of bird populations have for years been coupled with plant community surveys to obtain a measure of species response to vegetation. While these surveys will continue to be important in the future as they have in the past, they do not necessarily provide much insight into the detailed aspects of why one location seems more suitable for a species than some other location. Interest in this microscale problem as well as the theoretical underpinnings of habitat selection had been published quite early (e.g., von Uexkull 1909, Kohler 1947, Tinbergen 1951, Harris 1952). In the mid-1960's, there was an intensified interest in habitat selection as a behavioral phenomena (e.g., Wecker 1963, Klopfer 1965, MacArthur and Pianka 1966). This emphasis on individual organisms tended to produce observational data sets with very high degrees of freedom and with more than one variable recorded for each observation. Such data created a need to explore multivariate statistics as an analytical tool.

PROBLEMS INTRINSIC TO THE SYNTHESIS ELEMENTS

The synthesis of multivariate habitat selection methodologies proceeded from the combining of several elements of research from different fields in the 1970's. As a product of a rapid synthesis, today's procedures suffer from certain problems intrinsic to the component elements.

Statistical Assumptions Versus Niche Theory

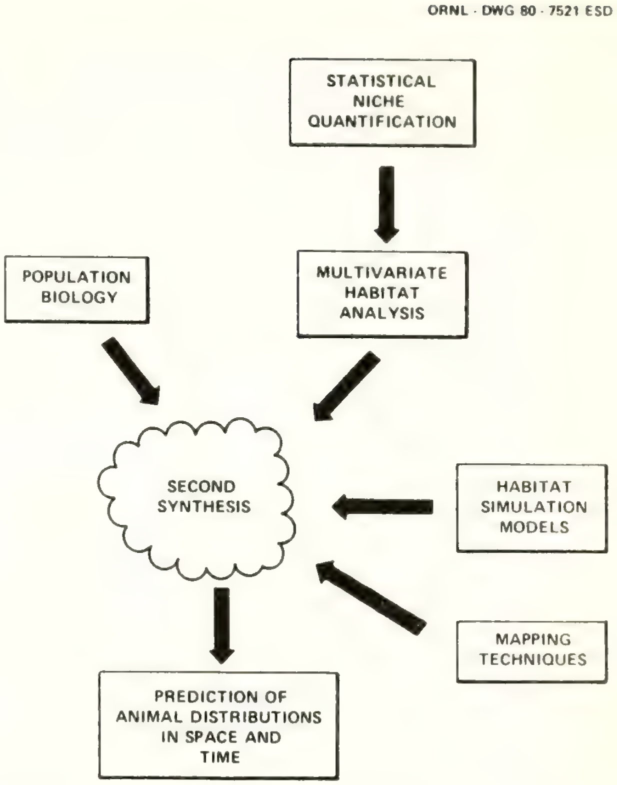
Multivariate habitat selection studies have a strong emphasis on using the "correct" statistical procedures. Most letters and phone calls that I receive regarding habitat selection involve deciding what method to use, not on how to interpret analytical results. Further, as contrasted to plant ordination studies in which authors typcially reference their methods to other ordination studies, multivariate habitat studies refer their methods to reputable multivariate statistical textbooks. This healthy respect for statistics is probably quite good, but it also makes papers in the field proceed with ponderous inevitability. I am of the opinion that rigorous adherence to methodological correctness probably has prevented incorporation of the heuristically rich geometric theories of the hyperspace niche concept from being fully developed in wildlife habitat studies.

Inclusion of Population-Level Aspects

Most multivariate habitat analyses are so focused on the responses of individual organisms to microhabitats that concepts of animal density are almost lost. Some species appear to be quite uncommon even in the face of an apparent abundance of suitable microhabitat. The Swainson's warbler (Limnothlypis swainsonii) is a possible example of such a species. It is difficult to include population dynamics in a detailed microhabitat study, yet such dynamics are essential to management of habitat for selected species. I believe that this will be one of the challenges to workers in this field over the coming decade.

Inclusion of Macrohabitat Considerations

The consideration of the pattern of microhabitats at larger spatial scales (macrohabitat) is difficult to include in the present multivariate habitat analysis methodologies. In fact, macrohabitat considerations are often viewed as an unfortunate sampling situation in which the sample space has a pattern of internal clusters. There may be considerable importance in arrangement of elements of the landscape that are suitable for maintaining viable populations of a species. Rosenzweig's (1973, 1974), Rosenzweig and Winakur's (1969), and Schroder and Rosenzweig's (1975) pioneering work on the theoretical and experimental responses of populations to altered patterns of microhabitats is an important benchmark set of studies that needs to be repeated in other communities.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STATISTICAL NICHE QUANTIFICATION
POPULATION BIOLOGY
MULTIVARIATE HABITAT ANALYSIS
SECOND SYNTHESIS
HABITAT SIMULATION MODELS
MAPPING TECHNIQUES
PREDICTION OF ANIMAL DISTRIBUTIONS IN SPACE AND TIME

Figure 2. Schematic diagram of scientific research elements that may combine to produce a second synthesis extending from multivariate habitat analysis.

THE ELEMENTS OF A NEW SYNTHESIS

In the previous section, I have tried to identify briefly some areas of new fruitful exploration for studies of habitat selection. There is a need to use the powerful methodology of multivariate habitat analysis to develop new theory, as well as to contine its use in difficult applications. In the former area, I believe that work I have been involved with in trying to develop a concept of niche patterns for communities (Shugart and Patten 1972) and particularly the development of this idea by my colleague Dr. R. D. Dueser (Dueser and Shugart 1979) are examples of attempts to extend from simple data analysis to theory. These proceedings hold great promise for stimulating other theoretical work and should definitely provide some classic examples of applications.

There is, in my opinion, a need for a second synthesis in the field and I would like to briefly identify what may be the important elements of this synthesis (fig. 2). First, there is a need to meld the exciting developments made in population biology over the past decade with the equally exciting developments in multivariate habitat analysis. The potential for cross-seeding these lines of research is great, and the only limitation in uniting the field is in the formidable mathematical development that must be unified between the two. Two important quantitative developments (the ability to simulate changes in microhabitats through time and computer mapping of habitats) are already beginning to be included in habitat studies, and two examples are provided below.

Habitat Simulation Models

One interesting development in the field of ecosystem modeling over the past few years has been the development of forest succession simulation models capable of providing extremely detailed predictions on the future states of forests (reviewed by Shugart and West 1980). The level of detail and spatial scale of the output of some of these models is similar to that used in multivariate habitat selection studies. This convenient parallel development opens the possibility of projecting the temporal pattern of habitat availability following either man-made or natural disturbances. Figure 3 is an example of such an application using the Appalachian deciduous forest succession (FORET) model (Shugart and West 1977) to project habitat conditions for the ovenbird (Seiurus aurocapillus) on Walker Branch watershed, a site of intensive ecological investigation located on the Department of Energy (DOE) reservation in Oak Ridge, Tennessee. The FORET model simulates the birth, death, and growth of each tree on a 0.085-ha circular plot. By collecting habitat data on the presence of the ovenbird that has corresponding habitat information to that predicted by the model, one can use the model as a habitat simulator. In this particular example, we used discriminant function analysis to classify habitat versus non-habitat. As can be seen from an example, one can also use the detailed succession simulator to perform model experiments such as projecting the habitat dynamics of a 22.9 cm (9-in) diameter-limit cut of commercially valuable species (fig. 3). Details of this particular methodology will be treated later in this volume (Smith et al. 1981). I mention this example here to identify a need for adding dynamics to our currently largely static methodologies.

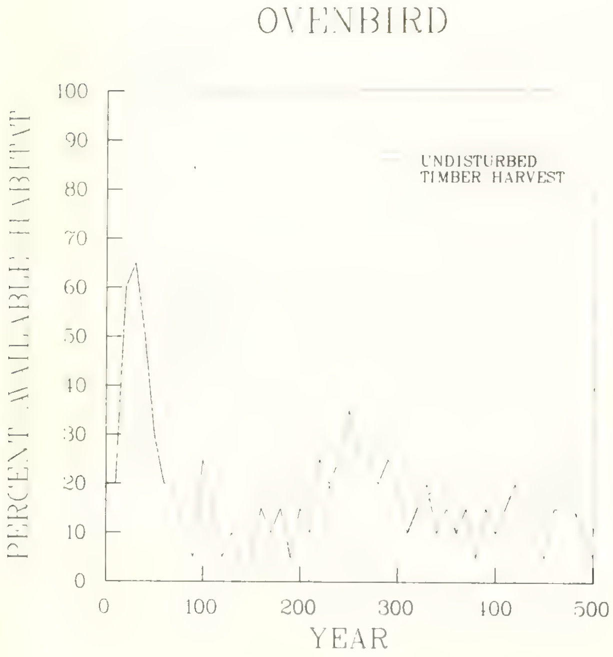

Figure 3. Ovenbird habitat availability over 500 years on Walker Branch Watershed under two treatments. Results are from the FORHAB model (Smith et al. 1981).

Mapping Techniques and Data Sets

There are presently a large number of data sets (e.g., the USDA Forest Service Continuous Forest Inventory [C.F.I.]) that could be used in conjunction with multivariate habitat data to make state- or continental-scale maps of distributions of wildlife habitat. The problems here involve keying habitat variables associated with a given species in a multivariate habitat study to the variables that can be obtained from inventory data sets. A fine example of this appraoch is Lennartz and McClure's (1979) application of C.F.I. data to map the potential extent of the red-cockaded woodpecker (Dendrocopus borealis) in the southeastern U.S. The determination of the level of variation over the continent of various species' habitat selection would be a valuable set of information for developing these maps.

THE SECOND SYNTHESIS

In this paper I have taken a broad view of the ontogeny of a still-developing understanding of habitat selection of several animals. The excitement of being involved in a young field is contagious, and I hope that this meeting will, by virtue of the increased interaction of scientists involved in multivariate habitat studies, help create a period of reviewed synthesis. The primary elements of such a synthesis might include the elements that I have mentioned (fig. 2), or they may take some entirely different direction -- only time will tell. Whatever the case, the present symposium should provide much fuel for the fire.

The healthiest aspects of multivariate habitat analysis have been of a philosophical rather than of a methodological nature. Studies have attempted to be rigorous in the sense of statistics while, at the same time, they have attempted to be both theoretical and explanatory.

This balance should not be lost. The studies have traditionally emphasized an understanding of ecological mechanisms at a fine scale of resolution. If such detail can be related to regional maps, the contribution to biogeography could be considerable.

In my opinion, the current research direction and velocity could, within the decade, provide such research products as dynamic maps of regional habitat availability for a great number of species, with the potential to determine the changes in these maps due to altered land-use policies.

ACKNOWLEDGMENTS

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DISCUSSION

MICHAEL C.S. KINGSLEY: Multivariate analysis tends to assume multivariate normality. Are there considerations in niche theory, particularly with respect to niche packing, which imply that niches should be a) similar in shape and orientation, b) similarly oriented multivariate normal density spaces?

H.H. SHUGART: Yes. R.M. May (1973. Stability and complexity in model ecosystems. 265 p. Princeton University Press, Princeton, N.J.) used the standard deviation and separation of means of species distributions along a continuum as an index of packing and overlap. He then determined ratios of these two statistics from derivations based on a general n-species non-linear competition model. He (Chapter 6) also provided a fair number of citations on niche shapes. In a somewhat less abstract vein, the late R.H. Whittaker generally pictured the distributions of species in response to gradients as unimodel and of shapes that are easily approximated by normal distributions. This is true both in his data papers, as well as in his more theoretical works. Whittaker used fairly abundant literature citations and his work serves as a useful point of reference. Maguire (1972) studied niche shapes in protozoa using non-parametric methods and found niches to have tendencies to vary along similar environmental axes and to have similar shapes. R.H. MacArthur and E.P. Wilson (1967. The theory of island biogeography. 203 p. Princeton University Press, Princeton, N.J.) produced a "compression hypothesis" regarding the expected similarity in shape and/or orientation of niches in different communities. W.E. Westman (1980. Gaussian analysis: identifying environmental factors influencing bell-shaped species distributions. Ecology 61:733-739.) provides a discussion on shapes of species' responses to gradients and also provides several references to individuals who have noted normal distributions in nature. A discussion with several citations of theories that would lead to such shapes is found in Westman's introduction.

THE USE AND MISUSE OF STATISTICS IN WILDLIFE HABITAT STUDIES[1]

Douglas H. Johnson[2]

Abstract.--This paper briefly surveys the application of various multivariate statistical techniques in studies of wildlife and their habitats. Several methods are widely employed, but with little regard for the requisite assumptions and often without full appreciation of what the methods do and whether they are appropriate for the problem or not.

The well known fact that species typically respond to an environmental gradient in a nonlinear fashion is poorly accounted for in many statistical treatments. Moreover, most analyses are not well validated. The few valiant attempts at validation have suggested that the models produced, often for predictive or management purposes, are less successful than might have been anticipated.

The use of multivariate methods in developing recommendations for wildlife management calls for special caution, for it is a major step from describing the relationships observed between a species and some habitat features to predicting the response of that species as the habitat changes.

Key words: Canonical correlation analysis; discriminant function analysis; multiple regression; nonlinear response function; principal components analysis; transformations; validation.

INTRODUCTION

The application of multivariate analysis to studies of wildlife habitat offers an exciting opportunity to statisticians. They have a major role to play as wildlife studies become increasingly complex and as greater numbers of environmental variables are investigated. A basic tenet of ecology is that "everything is connected to everything else." Although that generalization is a bit extreme, it does express the ecologist's conviction that the variables affecting a species or a system are numerous.

Faced with this acknowledged need for statistical service and counsel, statisticians must respond appropriately, which means carefully and thoughtfully, with a full understanding of the biological problem, and with an appreciation of the consequences of the statistical analysis and interpretation. Merely adding variables to an analysis will not do. Multivariate analysis must not be a masquerade for ignorance.

In this paper I survey some of the potential applications of multivariate analysis to wildlife-habitat studies. I try to offer biologists some guidance through the maze of multivariate statistics. My viewpoint is that of a statistician, with one eye on the mathematical requirements of the methodology, and one eye on the needs of the ultimate user--the wildlife manager. While looking in these two directions, we also must not forget the animal; its biology is of fundamental importance.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop. April 23-25, 1980, Burlington, Vt.

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IS MULTIVARIATE ANALYSIS APPROPRIATE?

Green (1971) identified the need for a multivariate approach when he mentioned three operational problems in defining the niche of a species: 1) Not all potentially important environmental parameters can be measured. 2) Many of the parameters measured are likely to be correlated, relatively invariant, or irrelevant to the problem. 3) The many potentially relevant variables result in a mass of multidimensional data that is difficult to interpret.

These considerations have led ecologists to the troughs of principal component analysis and discriminant function analysis, where they have drunk freely. These analyses have produced "new" variables that are linear combinations of the old ones, and which are fewer in number, to eliminate the third problem, a large mass of data. Further, these new variables are uncorrelated, which overcomes the second problem. It is left to the ecologist to handle the first problem by carefully including variables that are potentially important to the species; statistics will be of minimal help here.

These multivariate analysis overcome two obstacles, but not without their own disadvantages. One drawback is that, by involving linear combinations of all the measured variables, they do not really reduce the parameter space; all the original variables must be measured in order to calculate the new ones. In that sense, the analyses only provide guidance for future research. Another problem is that the linear combinations themselves may be extremely difficult to interpret. Many of the published ones lend themselves to meaningful interpretation, although some do not; and I suspect that a lot of unintelligible linear combinations have been lost somewhere between analysis and publication.

I wonder if we can take a slightly different approach. Can we objectively define meaningful variables *a priori*, instead of doing so statistically, *a posteriori*? These new variables should be few in number, more or less uncorrelated with one another, and of potential importance to the animal. These variables would account for what is known (or believed) about the animal, and any additional variables that the analysis identified as significant would represent new findings worthy of additional investigation. For example, a bird might find James' (1971) outline drawings of niche-gestalts to be meaningful, and would be willing to select its habitat based on those drawings. But the bird would be hard-pressed to plug the values of 15 or 20 variables into a number of linear combinations, compare the calculated values to one another, and select a habitat with value closest to its liking.

Multivariate analysis, while evidently appropriate for wildlife-habitat studies, is difficult to apply and understand; Gnanadesikan (1977:2) suggested that univariate difficulties are raised to the pth power. He also identified some of the added problems and noted that much of the theoretical work in multivariate analysis, oriented toward formal procedures such as hypothesis tests on means, is of limited value for actual data analysis in the multivariate case. I next discuss some of the usual multivariate methods and their role in wildlife-habitat work, as identified by speakers in this workshop and earlier publications.

Discriminant Function Analysis

One of the most widely used multivariate techniques is discriminant function analysis (DFA), which is used to separate observations into groups on the basis of a set of measurements. In wildlife-habitat studies the observations are usually sites, and the groups denote whether a species was present or absent from the site, or whether species A was present as opposed to species B present. The variables are habitat measurements at the site. Lachenbruch (1975) is a valuable general reference and Tatsuoka (1970) presented a nontechnical exposition on DFA. Williams (1981) noted that DFA is applicable when the groups are well-defined and the set of measurements is ecologically meaningful. Groups of habitat sites defined by the presence or absence of a species are not always well-defined. At least three reasons for a species' absence can be identified: 1) the habitat at the site is unsuitable; 2) the habitat is suitable but the species is absent for other reasons, such as numbers in the population inadequate to occupy all suitable habitat or interspecific competition; or 3) the habitat is suitable and the site occupied, but the sampling procedure failed to detect it. DFA based on presence-absence data involves the implicit assumption that absence is due to the first reason above, but even in that situation the group corresponding to "species absent" may include sites where the habitat is unsuitable for different reasons (see subsequent section on Nonlinear Response Functions).

The requirement of DFA for ecologically meaningful measurements has already been addressed. My experience with biologists suggests that on the basis of their prior knowledge of a species and its habitats, they often can develop a very limited number of ecological variables that characterize occupied habitat. These variables tend to be combinations of two or more habitat measurements; for example, the breeding habitat of American woodcock (*Philohela minor*) might be characterized by a single variable expressing the presence of fertile soil supporting earthworms, vegetation dominated by shrubs or young trees, and the nearby presence of forest openings.

Ecologists should use their best information when defining habitat variables.

Williams (1981) emphasized the importance of equality of covariance matrices in DFA. More widespread is the notion, expressed by Klecka (1975:435) that DFA "is very robust and these assumptions (multivariate normality and equal covariance matrices) need not be strongly adhered to." Lachenbruch (1975) reviewed several studies and concluded that linear discriminant functions are satisfactory if the covariance matrices are not too different. If they differ considerably, then the appropriate technique is quadratic discrimination, which employs the unequal covariance matrices in the discriminant functions. Unfortunately, quadratic DFA requires large samples and is itself not robust to nonnormality. Most of the work involving DFA and its sensitivity to underlying assumptions has focused on the misclassification rates of the discriminant functions. In ecological studies the interpretation of coefficients is also important, but little is known of their robustness.

Principal Components Analysis

Principal components analysis (PCA) and closely related factor analysis are multivariate procedures designed to reduce the dimensionality of a data set. The purpose of the reduction might be to "stabilize scales of measurements" (Gnanadesikan 1977:6) by compounding several measurements of a similar nature into a fewer number that may be more stable, but I am aware of no ecologist who stated this as an intention. More often the purpose is for exploratory analysis, to screen out of many variables a few that are important. Bhattacharryya (1981) provided a general introduction to these methods; Gnanadesikan (1977) compared several methods including nonmetric and nonlinear ones.

Three problems specific to the application of principal components analysis in ecological work can be identified. First, I see little justification for selecting a linear combination of variables simply because it maximizes the variance within the total set, that is, it is a "best" summary. As Holmes et al. (1979) noted, one can increase the percentage of variance explained by the first principal component merely by adding redundant variables to the data set. As more and more of these are included, the principal components analysis appears better and better, but in fact only noise is being added to the system, and interpretation becomes increasingly awkward. A large percent of variance explained may reflect only ignorance in the selection of variables.

Second, PCA is not always useful in discovering the underlying structure of the variables. Armstrong (1967) presented an example involving 11 measures on rectangular boxes of various metals. All variables were functions of five underlying (and independent) factors: length, width, thickness, density and cost per pound. The PCA identified three factors that summarized 90.7 percent of the information in the original 11 variables. Despite an orthogonal rotation, the factors were not easy to interpret and the PCA was unable to reveal the rather simple basic structure of the data. It would seem unreasonably sanguine to expect PCA to be more enlightening in a complex ecological system. Karr and Martin (1981) presented another example, this one pertinent to biological data, that illustrated some hazards associated with the use and interpretation of PCA.

Third, there is no reason to assume that a principal component necessarily relates to the animal or its needs. The animal could be responding to one of the variables that is a minor component of all those that were measured. It seems more appropriate in most circumstances to use regression analysis with some measure of population density or "fitness" as the dependent variable. Smith (1981) suggested that canonical correlation analysis may also be useful in this regard.

In general, PCA offers a convenient way of summarizing a data set containing many variables. If the ecologist's purpose in measuring those many variables is to relate them to the presence/absence or density of a wildlife species, it is not obvious that the major principal components are the important ones. If most variables were selected because of prior knowledge about their relationship to the species, then these variables are likely to appear in the major components. It is conceivable, however, that a minor component may be important to the animal, and for this reason it is suggested that the species' response be examined in relation to each of the components. Factor analysis, which essentially deletes minor components, would not permit this examination and should thus be avoided in initial analyses.

Canonical Correlation Analysis

Canonical correlation analysis involves the linear relationship of one set of variables to another; it has had limited application to ecological problems. Smith (1981) reviewed these applications and discussed the technique and its shortcomings. He also provided a useful introduction to the literature. My own belief is that canonical correlation will continue to play only a small role in habitat studies. In addition to the reasons given by Smith, viz., difficulties in interpretation, large sample size requirements, lack of robustness to nonnormality, and assumption of linearity, the rationale for the technique rests upon the ecologist showing concern for a linear combination of "dependent" variables. Moreover, the coefficients in that combination are not based upon the biologist's intuition or interests, but are generated by the technique. How does one justify an interest in 2.07 robins + 0.16 brown thrashers - 1.92 chickadees? More likely the ecologist has a single dependent variable, or set of them, in mind, and univariate or multivariate regression is the more appropriate method.

Other Techniques

Regression has not been specifically addressed in this workshop, although it remains one of the most popular and powerful statistical tools for examining relationships among variables. The usual formulation of the regression model,

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k + \text{error},$$

where the X's are fixed input (or "independent") explanatory variables, is not strictly a multivariate technique; there is only one random variable, the error term. In actual practice, however, the X's are not fixed quantities (Johnson 1981) and the model can be viewed profitably in a multivariate light. If several species are to be examined in relation to a set of habitat variables, multivariate regression appears to be the appropriate method. Gnanadesikan (1977) discussed the method and noted (p. 81) that a multivariate viewpoint may be preferable to considering each dependent variable separately, because of intercorrelations among the dependent variables. Unfortunately, most multivariate regression work has focused on hypothesis testing (the general linear model) rather than model building.

In contrast to their botanical counterparts, wildlife ecologists have made little use of clustering techniques. Cluster analysis differs from DFA (a classification technique) by the lack of groups defined *a priori*; the groups are essentially defined by the clustering algorithm and the user is responsible for providing a reasonable interpretation of the resulting groups. Cluster analysis differs from ordination in the implicit assumption that units fit into neat and discrete groups, rather than being arranged in a continuum along one or more principal component or discriminant function axes.

Although multivariate techniques can be and have been rewarding in habitat studies, ecologists should not ignore the simple and powerful methods of univariate statistics. Careful analyses begin with graphical displays of the data for several purposes: detecting outlying observations that may be erroneous or would be inordinately influential on the analysis; selecting variables that appear to be important; checking the assumptions underlying particular analyses, such as normality; and suggesting appropriate transformations of the variables. Valuable references on graphical techniques include Daniel and Wood (1971), who emphasized the use of plots for detecting relationships between variables and evaluating fitted models; Mosteller and Tukey (1977), who employed graphs both for general display and for fitting of models; and Green (1979), who discussed and illustrated many graphs useful in ecological studies. Plotting is more awkward in the multivariate situation than in the univariate case, but methods are available (e.g., Gnanadesikan 1977). Among these are 1) two- and three-dimensional scatterplots of subsets of the data for studying separation within the sample, outliers, general shape and interrelationships; 2) probability plots of the observations on each response, useful for suggesting transformations; 3) scatterplots or probability plots onto principal components, and others. The longest journey begins with a single step. To insure that the direction of the trip is appropriate, that first step should be graphing the data.

Transformations

It is often necessary to transform variables in order to meet more closely the assumptions of various statistical methods, specifically those of normality, constant error variance, and uncorrelated errors. Other purposes are independent of the statistical properties, such as simplifying the relationship between variables or quantifying qualitative, count, or percentage data. Transformations may also maximize the separation between groups of observations.

Univariate transformations have received much more attention than multivariate ones; good expositions are given by Green (1979:43-54), Kruskal (1978:1044-1056), and references they cited. Kruskal (1978) offered some "clues" that suggest a transformation might be in order. Variables that approach an intrinsic boundary may be candidates for transformation; examples are percentages that closely approach 0 or 100 percent or correlation coefficients that come close to ±1. A nonnormal distribution can be detected by plotting observations on normal probability paper or by graphical procedures available in SAS (SAS Institute Inc. 1979) and other statistical packages. Nonconstancy of variance can be statistically tested for, but graphical procedures are more informative. Plots of residuals from fitted models may be made to suggest the presence of correlated error terms. Plots not only indicate the need for transformations, they also point out possible outlying observations. These may be data errors or at least data points more influential than the others.

The choice of an appropriate transformation, once one is recognized as necessary, is not quite as confusing as it might seem from the variety of those available. In many situations the choice can be made from theoretical considerations, such as the arcsine transformation for binomial data. In other situations a suitable selection can be made by examining the data; for example, the well known Box and Cox (1964) power transformation is a family of transformations indexed by a parameter that is itself estimated from the data.

Less guidance is available for transformations of multivariate data sets. This is unfortunate, because multivariate situations may require transformations more often in order to use familiar and simple analytic methods (Machado

1976). The choice of models in multivariate situations is more limited due to the general dependence on strict normality. The simplest approach to multivariate transformation is to treat each variable separately; this is likely to be a good first step at least. As Dunn (1981) noted for normalizing transformations, marginal normality does not insure multivariate normality, but the exercise is harmless at worst and is often quite adequate. Andrews et al. (1971) and Machado (1976) generalized the Box and Cox transformation to the multivariate case, and Dunn (1981) extended it to cover situations with more than one sample.

Transformations are often useful for obtaining stricter compliance with certain assumptions of statistical analysis. My own experience has demonstrated little advantage from analysis of transformed, as opposed to untransformed, data. Careful design to insure randomness overcomes many problems with correlated errors, and reasonably large and well-balanced samples mitigate the effects of nonnormality and nonhomogeneous variance (Green 1979:165). Transformations are advised, however, if they will clarify relationships or if the statistical assumptions are obviously violated. It certainly will not hurt to analyze the data both untransformed and transformed, and judge which analysis is superior.

NONLINEAR RESPONSE FUNCTIONS

It seems generally agreed that a species responds to an environmental variable, or to a gradient, in a nonlinear fashion. The form of the function could be normal, or of another symmetric shape, or it could be asymmetrical but unimodal, or it could even be bimodal. But it is nonlinear. Despite this wide acknowledgment, relatively little has been said about the effect of nonlinearity on the results of multivariate analysis (Westman 1980).

I wonder if we are like the several blind men, each touching a different part of an elephant, and reaching widely discrepant conclusions about the total shape of the animal. Suppose, for example, that a species responds to an environmental variable X as shown by the symmetric curve in figure 1. An investigator studying values of the variable only in region A would conclude that the species responds favorably to the variable; it is an "increaser." A study in region C would lead to just the opposite conclusion, while a study in region B would probably find that the species did not correlate at all with the variable. All conclusions are correct, and yet all are wrong. Even a study involving the full range of the variable, regions A plus B plus C, would detect no linear association.

A possible example is that of Converse and Morzuch (1981), who found that hare activity was correlated positively with the number of hardwood trees on one of their study areas, while the correlation with hardwood trees was negative in the other area.

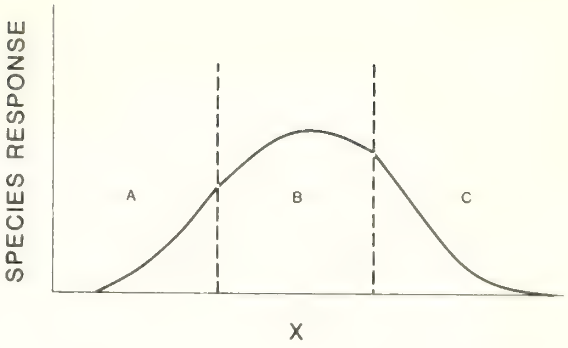

Figure 1. The nonlinear response of a species to an environmental gradient X.

In regard to discriminant analysis, Green (1971:544) suggested that a nonlinear response function might not be troublesome, because "species are groups separated in ecological space by linear additive functions of ecological parameters, rather than dependent variables supposedly related to the ecological parameters in a linear additive manner." I am not convinced that there is no difficulty, at least in some applications. Suppose, referring back to the response curve (fig. 1), that we form two groups: species Y present, and species Y absent. We want to distinguish these groups on the basis of their value of X. Most X values in regions A and C would fall into the species absent group, while region B would donate mostly species present. But it is evident that average values of X in the two groups might be very similar, even identical. For example, if the species is a mesic one and X represents a moisture gradient, then some sites might be too dry and others too wet. There are thus two groups in which the species is absent, and they differ more from each other than they do from the species present group. In higher-dimension space the problem only gets worse. Quadratic discriminant functions are theoretically applicable to such situations, but separating groups on the basis of variance when means are similar is tenuous at best.

In principal components analysis, or factor analysis, two problems related to nonlinearity occur. First, the methods produce linear combinations of the variables; if a nonlinear function is a better summary of the data, we will not detect it by the usual methods, although some nonlinear techniques have been developed (Gnanadesikan 1977). Second, if a species responds nonlinearly to a principal component, we had better be alert if we want to detect it, e.g., by plotting species responses against each component.

Nonlinear response functions can be detected by graphical tools and can be treated appropriately by nonlinear regression models (cf.

Boyce [1981], who eliminated from analysis a variable with a recognized nonlinear effect).

We must be particularly careful about nonlinearity when presenting our results to resource managers, who look assiduously for the "bottom line": What can a manager do? He might be told that opening up a closed forest yields more woodpeckers. He also needs to be told that this practice works only up to a point: complete elimination of trees will certainly have the opposite effect. We must remind him, and ourselves, that a management activity is like aspirin: just because two pills are good for us, it does not follow that four are twice as good, and a whole bottle is ideal.

STATISTICAL ASSESSMENT

I now turn to the question of how we might assess the statistical properties of habitat analyses. As a statistician, I am frequently appalled by the small sample sizes reported in many studies, particularly those involving large numbers of variables. Small samples of a complex system cannot support sound conclusions.

We are taught early in our statistical training to look, not only at the mean of a distribution, but also at its variability. In many published studies, however, we see species means plotted on axes of principal components or discriminant functions. Relatively few investigators mention the variation about those means; the few who have done so were very informative.

Conner and Adkisson (1977) plotted means of principal components for five species of woodpeckers; niche separation was shown among the species. When values for individual birds were plotted, however, they exhibited more overlap than might have been expected. Raphael (1981) also found considerable overlap among species on discriminant axes. Similarly, Smith's (1977) analysis of summer birds along a moisture gradient showed clear separation of 1% confidence regions for the means of eight species on two principal component axes. When plotted on the discriminant function representing a moisture gradient, however, values for individual birds of five species were scattered throughout, and relatively minor separation was evident. Researchers should meticulously examine the variability among animals.

Too little attention is given to annual variation in bird populations, fluctuations that take place seemingly without regard to habitat conditions, and certainly without regard to the unfortunate ecologist who is trying to determine relationships between habitats and populations. Ornithologists familiar with long-term studies can document the magnitude of this variation (e.g., Lack 1966, Wiens 1975), and I strongly suspect that it impacts habitat analysis. Rice et al. (1981) illustrated this problem nicely; discriminant functions developed from one year's data had few successes at predictions during the next year.

The use of stepwise procedures is viewed by many statisticians as a "fishing expedition." The standard significance tests are invalid (Draper et al. 1971, Pope and Webster 1972, Rencher and Larson 1980) and results are questionable, particularly in the usual situation of numerous variables. Automated computer procedures are no substitute for careful biological reasoning.

I believe that the application of robust statistical methods will offer considerable help in habitat analysis. McDonald (1981) gave details and references to the literature. Harner and Whitmore (1981) exemplified these methods and some internal validation tools, such as the jackknife and leaving-one-out procedures. In multivariate situations, applications of robust methods thus far have been primarily the treatment of one variable at a time (Gnanadesikan 1977:136), but this is likely to change in the near future. Particularly appealing is robustness of result with respect to method. If the same general conclusions are reached through the use of several different methods, each resting upon a somewhat different set of assumptions, we should feel more comfortable about the validity of those conclusions (Green 1977:14).

Validation is an important final product of an analysis. Whitmore (1977:263) stated that "the validity of ordination work can be tested by subsequent field observation." I agree, but such testing is rarely done. Noon and Able (1978) applied their discriminant functions for thrushes, developed for five species on Mount Mansfield in Vermont, to the two species occurring in the Great Smoky Mountains in Tennessee and North Carolina. They found little predictive ability.

The validation of models is particularly important if we are to present them to resource managers for their use. The need for caution on our part is obvious. In statistical parlance, management is really control, which is farther up the methodological ladder than description, inference, and prediction. As ecologists, our abilities on the lower rungs are as yet unproven.

A question that is rarely raised: What is the universe to which our results are to pertain? If it is a single study area, in a single year, with the measurements we have observed, there is no problem. If we want to generalize, let us be careful. Our study area must be representative of the area we want to extrapolate to, similarly the year, and the habitat. Noon and Able (1978) and Converse and Morzuch (1981) described how naive application of results from one area to another could be erroneous.

I see a clear need for experimentation. As observers of (more-or-less) natural populations of wild animals that do as they please, our options here are unforunately limited. But they are not curtailed. Is there a role for removal studies such as Stewart and Aldrich (1951) performed? An area which was repopulated soon after birds were removed would exhibit more of whatever the birds need than would an area that remained vacant. Habitat manipulation is another possibility. Some imaginative thinking might produce very valuable experiments to test the results we obtain from multivariate analysis of passive and uncontrolled observations.

MANAGEMENT APPLICATIONS

Multivariate analysis has been suggested as an important and useful tool in the management of habitats (e.g., Lennartz and Bjugstad 1975, Conner and Adkisson 1976, Evans 1978, Noon and Able 1978, Niemi and Pfannmuller 1979). It promises enhanced ability to examine a multitude of variables at once, just as a resource manager manipulates a multitude of habitat variables with the swing of an ax or the drop of a match. Clear-cutting a forest does not merely change the standing biomass of trees, it also affects stem counts, ground cover, litter, and a host of other measurable features: clearly a multivariate situation.

Again, I must sound a cautionary note. Are we looking at the right variables, and are we confusing association with causation? Consider the following paradigm. An action A, which may be either a natural phenomenon or a specific management activity, causes certain effects, denoted X_1, X_2, ..., X_n, upon the environment. One of these environmental effects, say X_1, in turn triggers a population response by a particular species, Z. Suppose we are observing the phenomenon, and record many of the environmental variables, but not X_1, and we record the response of species Z. Our analysis would show a relationship between the X's and Z; a multivariate analysis might reduce the set of X's to a smaller set of principal components, or discriminant functions, that also relate to Z. In truth, however, these associations are all spurious; the real association involves the "lurking variable" X_1, which correlates with the other X's and causes the response by species Z.

Even if we are clever enough to measure X_1 along with the other X's, the true relationship between X_1 and Z is almost certain to be clouded by the plethora of other variables. This paradigm is certainly not new; we have all been exposed to it in one form or another. But I believe we need to remind ourselves of it regularly; I am deeply concerned about the soundness of management recommendations based upon associations that are interpreted as causations.

The analysis may not always be misleading. In the paradigm just presented we might conclude that a particular configuration of X values is conducive to good numbers of species Z. The way to reach that X-configuration is by applying action A. This advice will work. Action A affects variable X_1, which in turn results in an increase of species Z.

But suppose there are other ways to obtain the desired configuration of X values without the appropriate value of X_1. Then that management action, even though it succeeds in producing the "correct-appearing" habitat, will fail to increase species Z.

As an example, fire produces certain effects in North Dakota grassland habitats, including removal of most standing vegetation and reduction of litter. The effects of the fire in turn produce a response by shorebirds; killdeer (Charadrius vociferus), marbled godwits (Limosa fedoa) and upland sandpipers (Bartramia longicauda) come to the burned areas to forage. Some range ecologists claim that appropriate regimens of cattle grazing will produce habitat changes similar to those caused by fire. Grazing could in fact produce similar measurements on a variety of vegetative parameters. But the shorebirds do not seem to respond in the same way to grazing as they do to fire. They must be keyed into one or more of the "lurking variables."

Other examples might contrast the effects of forest fires to those of clear-cutting, natural food supplies to artificial feeding stations, or natural pest control versus chemical control.

Rice et al. (1981) also pointed out how management practices directed toward one season can have possibly unintended and undesirable ramifications during other parts of the year.

Where we cannot design experiments freely, select optimal levels of variables at will, and replicate as often as we desire, we must be reserved about our findings. If management practices are adopted as a result of a multivariate habitat analysis, a thorough evaluation should be designed and conducted to determine if predictions from the proposed model are accurate and the model thereby remains tenable.

CONCLUSIONS

Multivariate analysis has been claimed to be useful in studies of wildlife and their habitats, despite the fact, clearly pointed out in this workshop, that the assumptions of the various methods are largely unmet. I see two possible explanations for this seeming inconsistency. The first is that biologists might be reporting the results of sophisticated multivariate techniques only when they are in accord with their biological intuition, previous knowledge, or results of simpler univariate analyses. A technique that produces conclusions in conflict with other knowledge may be rejected as inappropriate. If this is the case, then the multivariate methods are not truly useful; they only lend an appearance of further credibility to conclusions already reached from other directions.

A second possibility is that the multivariate methods might actually be more robust than is recognized. They may yield generally correct answers despite rather flagrant violations of their assumptions. Statisticians could be looking at finer detail than biologists do when they evaluate multivariate methods. A technique can be biased, of low power, inefficient, and defective in other statistical ways, but still provide valuable insight into the biological problem. One might define a technique to be useful if it produces more nearly correct answers than would be available without it.

It is for statisticians and biologists to work together in determining how useful various techniques are, relaxing assumptions that may not be critical, and designing studies to meet the assumptions that are truly needed. The papers and discussions have given a real stimulus to further cooperative efforts, and they will furnish guidance to researchers for many years to come.

ACKNOWLEDGMENTS

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DISCUSSION

E. JAMES HARNER: I disagree that multivariate analyses are almost always just exploratory. The jackknife and bootstrap techniques offer rather robust ways to make statistical inferences.

DOUGLAS JOHNSON: Multivariate techniques certainly can be used for inferential or, as I termed it, confirmatory research. As they are usually employed in wildlife-habitat studies, however, their proper role is exploratory.

JAKE RICE: From your figure it seemed that you pointed out that nonlinearity was a major problem in PCA, and you were talking largely about nonlinear responses of species (say abundances) to the environmental gradient represented by the principal component. Does not that sort of nonlinearily show up by simply graphing abundance against PCA scores? In that sense nonlinear responses are no more problem than in any univariate study where a species may also have a nonlinear response to any measure of an environmental attribute, and nonlinear regression methods are readily available. Is not the nonlinearity problem in PCA (and other multivariate techniques) one that the variables used in the PCA (say several environmental or habitat measures) may be interrelated in nonlinear ways?

DOUGLAS JOHNSON: You are correct on all counts. Nonlinearity of response is a potential problem whether the technique be univariate or multivariate. Nonlinearity can be examined by simple graphing, as you suggest and as I heartily recommend. A further difficulty with multivariate techniques, particularly principal components analysis, is nonlinear relationships among the explanatory (in our case, habitat) variables. If the relationships are present and strongly nonlinear, then the best linear combination of habitat variables may not be very good at all.

CHARLES SMITH: What is meant by "robustness"?

DOUGLAS JOHNSON: Robustness generally means insensitivity to violation of the assumptions of a technique. It has been further refined (Mallows, C.L. 1979. Robust methods--some examples of their use. American Statistician 33:179-184) to incorporate three concepts: 1) resistance--insensitivity to a moderate number of bad values and to inadequacies in the model; 2) smoothness--a characteristic of a technique in that it responds only gradually to the introduction of a few errors; and 3) breadth--the extent to which a technique can be applied in a wide variety of circumstances. A technique is called robust if it yields at least approximately correct answers despite having its assumptions not fully met.

RANDOM NUMBERS AND PRINCIPAL COMPONENTS: FURTHER SEARCHES FOR THE UNICORN?[1]

James R. Karr[2] and Thomas E. Martin[3]

Abstract.--Analysis of biological data with an array of multivariate procedures has increased in recent years. While these powerful tools have considerable potential for producing more rigorous biological conclusions, they are subject to misuse. We have analyzed real biological data and random number matrices using principal components analysis (PCA) and have shown that: 1) percent of variation accounted for may be similar for both, especially for the second and higher principal axes; 2) loadings of the original variables on principal axes are often as high as those for real data; and 3) matrix size is an important determinant of amount of variation extracted by PCA. The relevance of these and other points is discussed in light of the need for more objective grounds for the interpretation of PCA.

Key words: Bird/habitat relationships; principal components analysis; random numbers; sphericity test.

INTRODUCTION

This volume on multivariate statistics and wildlife habitat is the most recent in a series of publications demonstrating the power and value of multivariate procedures in analysis of ecological data. But, like so many other tools and/or dogmas in the ecological sciences, we feel it is necessary to reflect a bit on the potential for misuse of these "new" procedures. We urge caution in the use of one of the hottest items in the arsenal of multivariate procedures--principal components analysis (PCA).

Many researchers have used this procedure in the past decade for its major intended purpose--to reduce the complexity of multivariate data to a more manageable set of compound variables. This is not without some danger as no testing procedures are commonly used to allow measurement or evaluation of the significance of results generated by use of principal components analysis. Interpretation of pattern has commonly been based on relatively subjective grounds.

TWO DATA SETS

Our objective was to compare results of PCA on a matrix of real biological data with results from analysis of a random number table of the same dimensions. The size of data matrices used for analysis of bird/habitat relationships varies significantly among studies. For illustrative purposes we selected a matrix size of 10 x 24 because of an early use of PCA in bird/habitat literature (10 vegetation variables and 24 bird species). (Throughout this paper we refrain from citing specific studies. The questions we raise here are directed generally rather than at any particular study.)

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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Table 1. Percent of variation accounted for by the first three principal components for two 10 x 24 matrices.

Matrix	Percent of variation by component I	II	III	Cumulative
10 vegetation variables, 24 bird species	57	16	12	85
10 x 24 matrix of random numbers	25	14	14	53

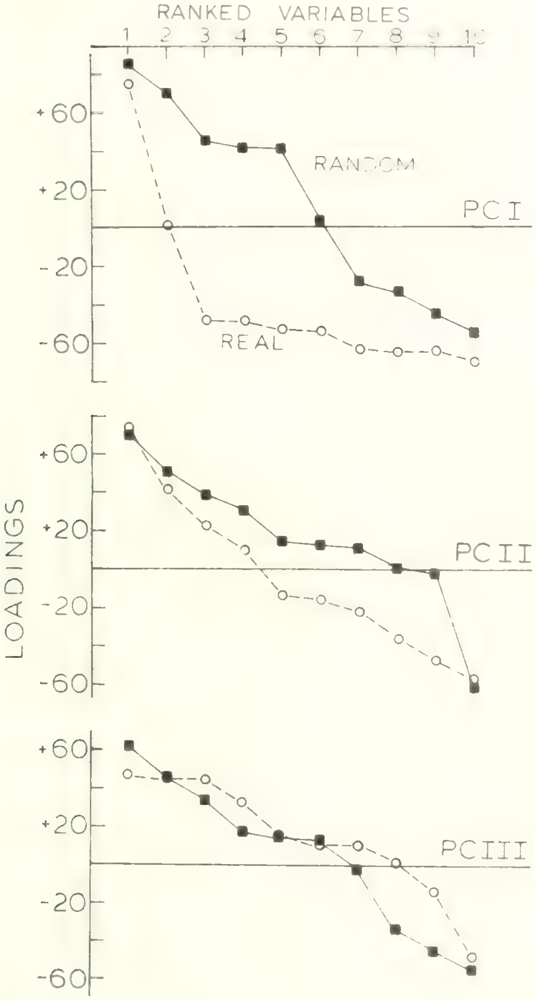

Figure 1. Distributions of loadings of original variables for principle axes I, II, and III for real biological data and random numbers (10 x 24 matrix).

For the real data matrix, 85% of the total variance was accounted for by the first three principal axes (table 1). However, use of PCA on an equivalent-sized matrix of random numbers extracted 53% of the variation in the first three components. Amount of variation accounted for in the real data was clearly very high, but it is instructive to view the situation from the opposite perspective. The percent of variation accounted for in a random number table was well above that which might be expected by the naive reader. A greater percentage of variation was accounted for by the first component for real data than for random numbers, but the second and third components accounted for similar amounts of variation in both real and random number matrices (table 1).

These results might tempt the reader to argue that loadings of original variables on the principal components must be much lower in the random numbers than the real data. This, it turned out, was not the case (fig. 1). Factor loadings had approximately the same maxima in the two matrices. We believe that most biologists would be able to generate a plausible post facto biological explanation of the high loadings in the random numbers for each of the three principal axes.

Although the maximum loadings of the original variables were about the same across the three principal axes for random and real data, the array of loadings over the ten variables was different for the first axis (fig. 1). Loadings for the random number and real data matrices were more similar in subsequent principal components. These results were due presumably to correlations among variables. The correlations among variables for real data include a greater number of high correlations than for random numbers (fig. 2). These high correlations allow the first component to account for a greater percentage of variation

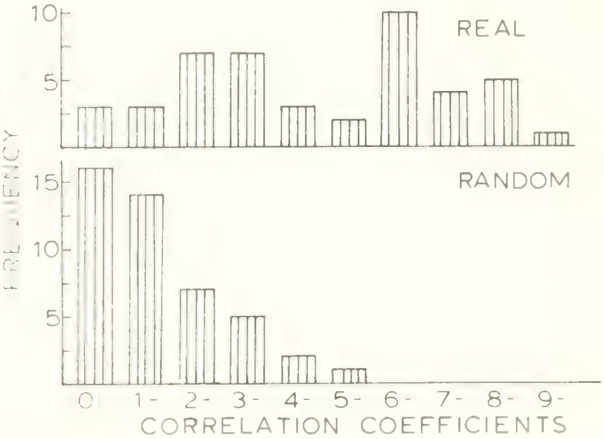

Figure 2. Distribution of correlations among original variables for real biological data and random numbers (10 x 24 matrix).

Table 2. Percent of variation accounted for by the first three principal components for real and random number (in parentheses) matrices of the same dimensionality. The real data examples are from published studies using principal components analysis.

	Percent of variation by component			
Matrix size	I	II	III	Cumulative
6 x 56	33(23)	22(20)	18(18)	73(61)
7 x 5	45(44)	23(28)	11(18)	79(91)
8 x 21	46(27)	17(20)	10(17)	73(64)
10 x 24	57(25)	16(14)	12(14)	85(53)
10 x 46	65(18)	12(16)	12(16)	85(50)
15 x 15	--*(22)	--(16)	11(13)	58(51)

* (--) indicates not available in original publication.

in real data. Thus, real data are more ellipsoidal in multivariate space than are random data which tend to be more spherical.

How, then, can we develop some confidence in the typically post facto explanations generated when real data are analyzed? As a first step, we suggest that authors and readers carefully interpret the percent of variation accounted for in a PCA by comparing the results with those obtained from a random number matrix of equal dimensions. One possibility might be a table of expected amount of variation accounted for by random number matrices that could be used as a test relative to the amount of variation accounted for in real data. Another possibility is the sphericity test described by Pimentel (1979). This procedure tests the equality of components. When three or more axes are of similar length, they define a sphere in which axes are arbitrarily placed. Thus, components may be uninterpretable when they are equal. Finally, there are other tests available when analysis is based on the covariance matrix. For instance, the equality of a vector based on biological data and a theoretically derived vector can be tested (Pimentel 1979). However, since most biological PCA's have been based on correlation matrices, we confine discussion to these analyses.

The sphericity test simply tests the homogeneity of the last p - k factors, where p is the total number of factors and k is the first k factors not being compared. The homogeneity of the second and third factors can be tested if the first three factors are transformed by subtracting the mean eigenvalue of the last p - 3 factors. Analysis of results from the 10 x 24 matrix (table 1) with the sphericity test shows that the second and third axes are equal for real data ($\chi^2 = 0.604$, $P > 0.05$). Thus, real data appear to exhibit a primary ellipsoidal pattern (axis 1) but not in subsequent axes, so interpretation of axes 2 and 3 may be invalid.

OTHER MATRICES OF BIOLOGICAL DATA

We selected several published studies to illustrate the similarity of results from real and random number data. Much variation is explained by random number matrices relative to real data of the same dimensions, especially in situations with few variables (table 2). These results lead us to urge caution in using PCA for small matrices, a proviso on sample size similar to that for normal univariate statistical procedures.

As in the earlier example, the trend for a greater difference in the first axis but similar results for the second and third axes of random and real numbers seems to apply across a variety of matrix sizes (table 2). However, note that although the percent of variation accounted for in the real and random data is similar for the second and third axes, this is partly due to the first component of real data accounting for a greater percent of variation than in random numbers. This leaves less variation to be accounted for by the second and third components in real data. Real data account for a greater proportion of the remaining variation than in random data for large matrix sizes. For example, in the 10 x 46 matrix, the proportion of remaining variation accounted for by the second (real - 34%; random - 20%) and third (real - 52%; random - 24%) components is higher for real data. However, for the 7 x 5 matrix, the proportion of remaining variation

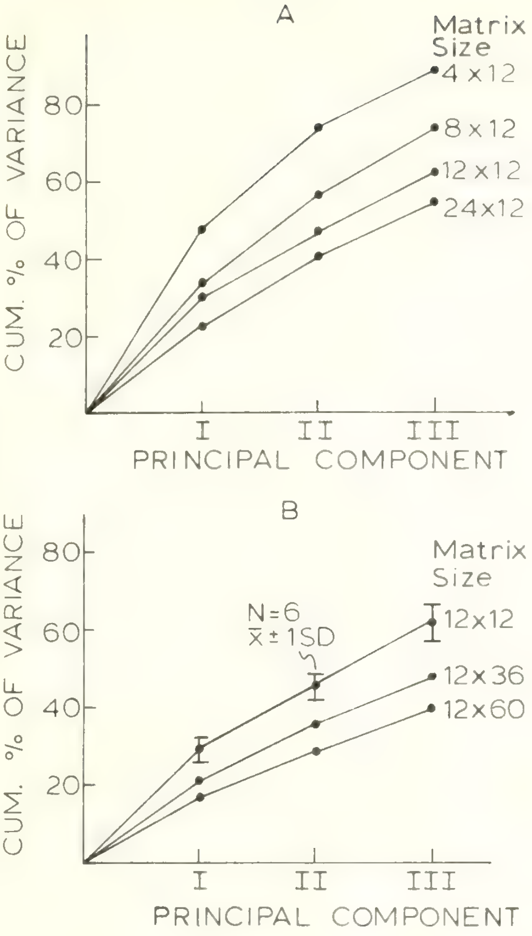

Figure 3. Cumulative percent of variation accounted for in principle component analysis of random number tables of various sizes.

accounted for by the second (real - 42%; random - 50%) and third (real - 34%; random - 64%) components is greater for the random data. While the pattern is of interest, we know of no statistical procedures that can be used to test its significance. At the least, the pattern emphasizes the need for caution when using PCA on small matrices.

Even if the second and third components explain a greater proportion of the remaining variation in real data than in random numbers, it may be difficult to apply biological interpretations to these axes if they are equal. The sphericity test indicates that the second and third components are not significantly ($P > 0.05$) different in any of the studies in table 2. One is tempted to conclude that, in bird/habitat data, the first axis reflects the presence of a primary ellipsoid while subsequent axes are nearly as spherical as a random numbers matrix of the same dimensions. If this is true, interpretations of components subsequent to the first may be invalid; at the least, they should be tested by the sphericity test before they are interpreted in great detail.

THE EFFECTS OF MATRIX SIZE

Obviously, the amount of variation explained from random numbers varies with number of derived axes since 100% of the variation must be extracted from a number of axes equal to or less than the number of variables in the analysis. For example, a matrix of 10 vegetation variables with 24 bird species must yield 100% variation in 10 or fewer axes. Typically, all variation is extracted with fewer components than variables. When there are few variables, the problem becomes especially critical (e.g., 89% on the first three principal axes in a 4 x 12 matrix; fig. 3a).

Similarly, when the number of variables is held constant but the number of cases varies, the percent of variance accounted for declines with increasing matrix size (fig. 3b). Note also that variability among random number matrices of the same size is rather small (fig. 3b).

DISCUSSION

We must emphasize that our purpose is not to convince the reader to avoid using principal components analysis. Rather, we hope to inspire more critical evaluation of the uses and misuses of PCA. When the amount of variation accounted for from an axis or set of axes is similar to the amount from random numbers, we question the biological validity of interpreting those axes.

Canonical correlation (CanCorr) analysis is similar to PCA in its analytical procedures except that CanCorr is developed to analyze the relationship between two data sets. In addition, CanCorr includes a test of significance of the canonical variates. We have applied the test to random number matrices of a variety of sizes; no significant ($P > 0.05$) canonical variates were found. Most biologists would probably not try to apply biological interpretations to such results. Use of a similar decision-making process is needed in the use of PCA.

Finally, we note that similar results from principal components analysis of random and real data do not necessarily mean that biologically important relationships are not present. However, it is important to use sound biological judgment in the interpretation of the results. The final test of the procedure in any circumstance is the biological insight developed. That is, the results of PCA should not be used simply for post facto interpretations, but rather to aid researchers in generating reliable predictions and viable hypotheses which are testable with additional research.

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DISCUSSION

JAKE RICE: In defense of the use of these methods, in this case PCA, I can at least say that the field of statistical ecology has progressed to the point where one usually cannot get a paper published just by doing a PCA on a data set and writing up the result. If the factor loadings make biological sense, like Smith's forest moisture gradient (Smith, K.G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark Watershed. Ecology 58: 810-819), then one has some results to work with. If the loadings and the scores do not make sense, one goes back, or should go back, and look hard at the system; obviously one's understanding (and data base) of the system are incomplete.

If you also randomly assigned habitat names to "variables" and site names to "samples," in your random matrix; factored it; and could put a plausible biological explanation on the results, then I would be surprised.

JIM KARR: Many users of PCA and other multivariate procedures have progressed beyond the "fishing expedition" approach but others have not. The questions posed in this paper are directed toward both groups--primarily as a caution about interpretation and use of results. They should not be construed as suggestions to avoid the procedures and the new insights they can produce if used wisely. A problem inherent in PCA is the lack of objective statistical tests to determine the significance of the patterns which "make sense." Note that both statistical and biological significance are of concern; they may not be the same.

We clearly disagree with your final point. I am confident that most biologists could generate plausible "post-facto" explanations for high loadings after randomly assigning habitat names to the "variables" in random number tables. The small sample of examples that I have seen clearly demonstrate the ingenuity of biologists in that regard.

CHARLES SMITH: We typically assume that there is a pattern of some kind; and when none is detected, we question the validity of the techniques. What if the most easily detected pattern is one in time, not space, and the spatial case is not detectably different from a random pattern, in the absence of a time-series sample?

JIM KARR: This is a real problem. Indeed, I have fallen into that trap myself. After one year of study in forests in Panama, I concluded that individuals and species moved extensively among microhabitats in lowland forest. Long-term data show that to be true but the subtlety of habitat selection is exceptional. The use of specific microhabitats varies between seasons and years in ways that are quite predictable from knowledge of environmental conditions (wet vs. dry dry season) at the time. Lumping of data for many kinds of statistical analysis can result in the error you mention (i.e., assuming a lack of pattern when a pattern, in fact, exists); that simply reinforces the point that statistical analyses should always be guided by biological knowledge (insight).

Special Session: Sampling Avian Habitats

RATIONALE AND TECHNIQUES FOR SAMPLING AVIAN HABITATS: INTRODUCTION[1]

James R. Karr[2]

Three more or less distinct (but overlapping) stages might be recognized in the development of studies of avian habitats. The first "Catalog Stage" began with efforts to identify birds and determine their phylogenetic and biogeographic affinities. Habitat descriptions were generally cursory and nonquantitative. For example, the monumental Manual of Neotropical Birds (Blake 1977) describes the habitat of the red-tailed hawk (Buteo jamaicensis) as "Mainly woodland and semiopen country."

During the second "Natural History Stage" scientists were interested in general biology or natural history of species: nest type and location, food habits, clutch size, incubation period and general habitat were of primary interest. Few efforts were made to provide quantitative information on avian habitats; the main focus was the bird itself. The classic works of Nice (1937) on the song sparrow and Skutch (e.g. 1969) on neotropical birds are examples which focus on the natural history of birds, including nonquantitative studies of their habitats.

In the third "Ecology of Habitat" stage emphasis shifted to interest in both the birds (often as communities) and their habitat (vegetation type). The importance of foliage structure in determining avian use of habitat has long been recognized (Merriam 1890, Grinnel 1917, Lack 1937, Pitelka 1941, Kendeigh 1945, Svardson 1949). The first quantitative and graphical demonstration that vegetation of increasing height and complexity typically supports increasingly diverse avifaunas was provided by MacArthur and MacArthur (1961). Many refinements of this approach have been developed in the past two decades. Some are appropriate for consideration of single species, while others are more appropriate for community level studies.

Increased emphasis on quantitative approaches to the study of avian habitats has precipitated some innovative uses of quantitative methods. Use of information theory was pioneered by Robert MacArthur and has continued with the work of others (Recher 1969, Karr and Roth 1971, Blondel et al. 1973). Other efforts to demonstrate a relationship between foliage height diversity and bird species diversity have been less successful. Some failed because of inappropriate measures of habitat structure. Others failed in habitats where the rules of plant geometry and distribution are different. For example, foliage volume is important in some situations (Sturman 1968, Laudenslayer and Balda 1976), while life form diversity of plants is more important in others (Tomoff 1974). Further, precision of relationships between habitat structure and avian diversity is often less precise when narrow ranges of habitat structure are examined (Lovejoy 1974, Willson 1974).

An array of multivariate statistical procedures also are being used in studies of bird-habitat relations. In general, these techniques (principal components, discriminant function analysis, reciprocal averaging, canonical correlation) have the attribute of reducing many variables to a small set of complex variables. Other attractive features include easy development of graphical presentations and studies of how variation in one variable affects birds when other variables are held constant.

Multivariate methods are not without problems, however. First, like most univariate methods, they are merely descriptive procedures. They are essentially correlation techniques and cannot be used to determine casual (ultimate or even proximate) relationships between birds and their habitats. Although complex data transformations result from use of multivariate procedures, it is not always clear how to extract biological (vs. statistical) meaning from these correlations. Further, the caution that ecology is the art of describing the obvious is also relevant. There is a tendency to use multivariate methods to demonstrate phenomena which are already obvious from univariate studies. The true test of a procedure is its ability to generate new predictions about biological phenomena, to go beyond the obvious. Application of multivariate methods cannot substitute for in-depth consideration of the biology of the organisms under investigation. Careless use of these procedures has stimulated one biologist to comment that so much mathematical formality combined with so much ecological casualness is puzzling (Beals 1972).

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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THE DEFINITION OF HABITAT

Use of the concept of habitat by a single investigator (and among investigators) is often inconsistent (Karr 1980). At least three major meanings of habitat commonly can be discerned:

1. Habitat = vegetation type (grassland, forest, etc.).
2. Habitat = the living and non-living surroundings of an organism.
3. Habitat = specific horizontal (vegetation configuration) or vertical (twig angle, leaf density, etc.) components of vegetation structure. These are often referred to as the microhabitat of the species.

Obviously, it is not possible to address all of these and other difficulties involved in the analysis of avian habitats in a few short papers. However, the papers that follow outline many of the problems and propose some innovative solutions as guides for the future. Presentations are organized around three major questions:

1. Why do we measure habitat?
2. What habitat variables should be measured?
3. How do we measure those variables?

The "why" question must generally be answered first. The answer will place constraints on the "what" question (and so on to the "how" question).

THE "WHY" QUESTION

In addressing this question Rotenberry provides the simple answer: It works. He argues that it works because habitat forms the background upon which all adaptive patterns are expressed. Further, it works for a wide range of studies. Successes using the habitat approach include both basic and applied objectives; single species, several species, or entire communities. The need for quantitative habitat assessment is especially critical in efforts to preserve endangered species. Since the type of "why" question helps define approach, sampling protocols, and nature of data analysis in any study, dealing with the "why" question is an important first step.

THE "WHAT" QUESTION

Since not all relevant parameters can be measured in any study, researchers must restrict the "what" to strike a balance between time and money constraints and the need of a sound research design with high probability of developing useful conclusions. Exact variables to be measured, as well as how precisely they will be measured, vary with study objectives. The emphases of the two contributions here are toward theoretical and applied considerations. In the applied situation, a reliable correlation between a habitat variable and avian patterns of interest may often be sufficient for management decisions. Whitmore's presentation makes the point that sound research design directed toward a distinct management objective can yield results of major significance for management to enhance wildlife populations.

In a theoretical context, it may be more important to understand the causal links relating habitat and avian species or communities. Thus, a theoretician may need to sample insect (or other food) abundances in space and time to understand complex relations between physical environment, vegetation structure, food supply, and avian habitat use. This more complex picture may be necessary for a rewarding exploration of ecological and evolutionary causes of patterns in avian species and communities. In addressing this question, Holmes outlines examples to show the need for more rigorous procedures in determining which habitat variables should be measured. He argues strongly for the need to consider natural history of the study organism(s) in determining variables to be measured. Based on this principle, he outlines several difficulties with current approaches and cautions that more detailed and precise information is needed before truly scientific management can be accomplished.

THE "HOW" QUESTION

The answers in a specific case to the "why" and "what" questions narrow the options in the "how" question. In some cases, superficial (perhaps even nonquantitative) measures of very general factors are all that is required; in other cases, detailed and comprehensive measurements may be necessary. Both biological and statistical constraints must be kept in mind at this stage. Noon's extensive experience with sampling avian habitats leads him to propose a variety of specific protocols for use in several circumstances. His proposals are a valuable mix of techniques which have proved successful for a number of researchers. He calls for efforts to standardize some procedures to facilitate comparisons among studies. While there is some merit to this point, I urge caution in too firmly establishing a sampling protocol. It is premature for protocols to be "chipped-in-stone" in such a rapidly developing area. Some adoption of sampling conventions should be attempted, but the way for improvement of those procedures should be kept open as knowledge of the relations between birds and their habitats is improved. In the final paper of the series, Johnson urges biologists to make study design decisions with a clear view of the objectives and goals of each specific study. He contrasts exploratory and confirmatory research, while urging that conclusions be based on sound scientific design (hypothesis testing, etc.) and not fishing expeditions for significant correlations.

Finally, I would like to reiterate the point that all insights will not depend on use of complex multivariate procedures. Although that is the general subject of these proceedings, it is important that we reflect on the reality that the final measure of value for a study or technique is whether or not it yields insight into the dynamics of the ecological systems that we are studying.

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WHY MEASURE BIRD HABITAT?[1]

John T. Rotenberry[2]

Abstract.--The rationale behind studies that attempt to assess bird/habitat relationships quantitatively is structured around the premise that a bird species' habitat selection is of adaptive significance. This rationale was originally posited by Grinnell and led to the development of the concept of "niche". Although the definition and use of the term "niche" have undergone substantial expansion, it seems clear that habitat variables (especially those associated with vegetation structure) do represent an integral part of bird species' niches. By comprising either proximate or ultimate factors to which species must respond, habitat forms the background upon which all adaptive patterns are expressed. Thus a full understanding of the evolution of species' ecological attributes can come only in association with precise quantitative descriptions of environmental conditions.

Key words: Adaptation; birds; Grinnell; habitat measurement; habitat selection; niche.

INTRODUCTION

With maturation of natural history as a science, it is apparent that information of a general descriptive or quantitative nature about habitat is absolutely essential for a full understanding of patterns of life history, adaptation, and evolution of any species. This seems especially apparent for birds. As I perceive the role of this paper, it is not to state that the reason you should measure bird habitat is because it "works," then proceed to provide you with an exhaustive list of examples; indeed, many of the contributors to these proceedings are responsible for those examples, and their reiteration would prove superfluous. Instead, I shall attempt to summarize briefly some of the rationale behind why we think it "works," structured around the notion that an organism's habitat reflects aspects of its adaptations.

NICHE CONCEPTS

With birds, perhaps more than for any other taxa, there has been a historical as well as a theoretical component to why we gather habitat data. The seminal paper in bird/habitat relationships, and indeed for much of ecology today, is Joseph Grinnell's classic study of the California thrasher (Toxostoma redivivum) (Grinnell 1917). Grinnell introduced two important concepts that have formed the foci for the way we think about birds and their habitat relationships. The first of these, of course, was the creation of the term "niche" and its conceptualization as a close association between distributional patterns of a species and the underlying environmental conditions. The second was the notion that niche relationships were important not only in telling us about adaptation and natural history of whatever organism we are describing, but also in revealing aspects of its relationships to other organisms and, ultimately, of the structure of the community in which it resides. The latter idea has received more emphasis in a theoretical context, largely under the construct of the n-dimensional hypervolume model of Hutchinson (1958). Both of these concepts, the niche as habitat and as something that reflects individual adaptation and community organization, form the basis for the sorts of questions addressed in these proceedings.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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Grinnell's original concern was to explain the rather restricted ecological distribution of the California thrasher. He thought that reasons could be found in the various physiological and behavioral adaptations of the bird to a narrow range of environmental conditions. It seemed evident that the nature of these critical conditions was to be learned through an examination of the bird's habitat. From this Grinnell went on to relate various aspects of thrasher biology and distribution to certain physiognomic, floristic, faunistic, and climatic features of the environment, and described these as the "niche-relationships" of the species.

Since Grinnell, niche has been redefined several times, with most of these reformulations stressing some aspect of the functional role of the organism within the community (e.g. Elton 1927). Some have even argued for a strict separation of a species' habitat and function, with the former representing environmental relations and the latter the "true" niche (Whittaker et al. 1973). It seems more probable, however, that these ideas simply represent ends of a continuum, with substantial intergradation between the two. Insofar as birds can be shown either to partition or to select different subsets of habitat within a community (e.g. Cody and Walter 1976), those differences in habitat among them will provide indications of the differences in their functional roles. It seems clear, then, that habitat variables do represent an integral part of a bird species' niche regardless of the presumed rigor of one's definition of the niche in general; indeed, numerous aspects of niche theory have been elaborated in just this context (Shugart and Patten 1972).

HABITAT SELECTION

Of course, the ornithologist's approach to the concept of habitat as niche has evolved through the years as well, but it still embodies the basic assumption that a predictable relationship exists between the occurrence of a species and certain characteristic habitat requirements. The current approach is often to focus on the floristic or vegetational structural aspects of avian habitat, what James (1971) has termed the "niche-gestalt." The concept of niche-gestalt is predicated on the theory that there is some basic configuration or pattern in the environment that an individual animal will seek out and settle in. This habitat selection process may be based on a specific search image, early learned experience, the particular genetic make-up of the individual, or any combination of these factors (Klopfer 1970). Presumably, then, habitat selection is an evolutionarily derived mechanism that insures that individuals seek out and remain in the particular environment to which they are adapted. This implies, in turn, that the result of habitat selection, that is, the association of a particular species with a particular subset of an otherwise vast environmental landscape, will reflect major aspects of a species' ecology and behavior.

The recognition stimuli that induce a bird or any other animal to select a particular habitat may often appear to be unrelated to the actual survival and successful reproduction of that organism (Hilden 1965). Such proximate factors achieve importance less through direct influences on the animal's biology than through correlation or association with the ultimate factors that are influential, in an adaptive sense. It is the latter that are essential to survival and constitute the underlying selective pressures to which the species is adapted. In many respects, then, the niche-gestalt is that set of proximate factors that elicits a habitat selection response (Smith 1977). These factors are presumed, in turn, to provide the birds with predictive evidence of ultimate factors. For birds, the physical structure of the habitat has long been considered to be an important proximate niche dimension, either directly, as it provides shelter, nesting substrate, or protection from predators, or indirectly, as it provides cues to the potential availability and diversity of prey (Wiens 1969).

In dealing with habitat physiognomy, ornithologists generally consider the measured parameters to be representative of proximate aspects of the niche. From the readily observable proximate relationships, however, we then inductively create hypotheses or models that often deal with functional elements of the niche, or the species' role within the community. Again the "habitat" and "functional role" aspects of the niche concept seem intertwined rather than exclusive alternatives. If there is a relatively good correspondence between the proximate and ultimate factors, then from these hypotheses and models we can deductively create testable predictions about other relationships between birds and their environment, or even between sets of bird species.

Although the very concept of "niche" has been challenged by some ecologists as being trivial (e.g., Ricklefs 1973: 522), it is clearly on the merit of its usefulness as a model or predictive tool that it should stand or fall. It seems quite clear for birds, at least, that the notion of habitat as niche has been extremely useful. Perhaps the most direct manifestation of this is the relative ease with which numbers of individuals or relative densities of many bird species may be predicted from measurement of habitat variables (e.g., Anderson and Shugart 1974, Robbins 1978). Likewise, the simple presence or absence of a species may often be strongly correlated with a suite of environmental measures (e.g., Smith 1977). Such relationships have been empirically and statistically verified many times, and some bird/habitat relationships are so strong that field identification guides may use habitat occupancy as a key character (Robbins et al. 1966). If in fact habitat selection does represent a major evolutionary component of avian natural history, then these correlations may allow us to make predictions about the adaptations of particular species. We may also identify species that depend on rather specific habitat conditions (what we call narrow-niched species, or specialists) versus those that are associated with a wide variety of conditions (broad-niched, or generalist species). Through this relationship we may again infer adaptive relationships.

Such correlations and associations between single species of birds and habitat variables are also of substantial practical value. They allow us to predict with varying degrees of accuracy the response of a species to natural or artificial habitat alterations. They permit us to identify species that, because they are relatively specific in their habitat requirements, are most likely to undergo major population declines if certain portions of that habitat are altered. And finally, they allow us to identify environmental management practices that may increase the amount of appropriate habitat for species that have become endangered or rare as a result of previous habitat loss.

COMMUNITY COMPOSITION

On a large scale, niche theory and the distribution of species along environmental gradients allow us to make predictions about the coexistence or co-occurrence of species in communities. To the extent that species are distributed along a habitat gradient more or less independently of one another, the community composition of a site is predicted merely by its location along that gradient (Rotenberry and Wiens 1980). Niche theory suggests, however, that under certain environmental conditions species may not vary independently from one another, but instead that inter-populational interactions, such as competition, will contribute to the nonrandom distribution of species along habitat gradients (Terborgh 1971). This, of course, has proven to be a fertile area for theoretical speculation and prediction, and the role of competition in organizing bird communities, expressed through either habitat displacement or, conversely, coexistance mechanisms, has been investigated extensively (see especially Cody 1974). Regardless of whether one chooses to look at community composition as a result of the independent distribution of species on environmental continua or the product of intense competitive interactions leading to tightly ordered distributional patterns, it seems clear that the nature of the underlying habitat will have a profound effect on community composition. This observation is perhaps best exemplified by what has become virtually a truism in avian ecology: bird species diversity may be regularly predicted from vegetational complexity, as expressed through either plant species diversity (Lovejoy 1974), life form diversity (Tomoff 1974), or structural diversity (MacArthur and MacArthur 1961). Of course, it will be only through careful measurement of appropriate habitat variables coupled with knowledge of species' biologies that we will be able to distinguish the independent versus competitive alternatives.

CONCLUSION

Quite beyond all these other reasons that I have outlined as providing a rationale for measuring bird habitat is the simple observation, as I indicated at the outset, that the measurement of habitat does seem to "work" for birds. By "work," I mean that there appear to be regular, repeatable patterns of associations or correlations between birds and habitat variables, regardless of any theoretical expectations or interpretations. Empirically this is verified by the literally hundreds of papers that have appeared since Grinnell that demonstrate nonrandom occupancy of habitat. These documentations may range from things as simple as the correlation between sagebrush coverage and sage sparrow (Amphispiza belli) density in the Great Basin (Rotenberry and Wiens 1978), on up through a detailed elaboration of the relationship between foliage height diversity and bird species diversity in a tropical forest (Karr and Roth 1971).

The message I wish to convey is simple: if we are to discuss any bird species' ecology in an adaptive context, information about its habitat is essential. This is because habitat forms the background on which all adaptive patterns are expressed. Virtually all attributes of a species, from its internal physiology on up through its interaction with other members of its community, have evolved for certain environmental conditions. Without knowledge of those conditions, which is expressed through our quantitative or qualitative description of habitat, the adaptive nature of these attributes is unknown. It seems apparent, therefore, that the necessity of defining these environmental conditions will result in the continued intertwining of bird populations and habitat measurements throughout all phases of avian ecology.

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THEORETICAL ASPECTS OF HABITAT USE BY BIRDS[1]

Richard T. Holmes[2]

Abstract.--For the theoretical ecologist interested in understanding why correlations exist between the occurrence of bird species and certain habitat variables, it is necessary to know how birds use their habitats. Such information also provides the basis for choosing appropriate habitat variables to measure. These points are illustrated by observations of birds in a deciduous forest in New Hampshire, in which different species of trees are found to be important habitat parameters.

Key words: Bird foraging; factor analysis; Hubbard Brook; vegetation structure.

INTRODUCTION

A major goal of the field of avian ecology is to develop an understanding of the factors that determine the patterns of occurrence, distribution, and abundance of birds. With respect to habitat, the avian ecologist is specifically concerned with why birds occur where they do, why there are correlations between bird species distributions and certain habitat variables, and particularly what are the ecological and evolutionary causes of these relationships and patterns. Since it is important to understand the causal relationship underlying the observed patterns before devising or implementing a management plan, such information is also of direct use to the wildlife ecologist/manager who is interested in manipulating bird habitats.

In this paper, I review briefly some of the protocols and procedures used in studies of avian habitats in terrestrial, mainly forested environments, and recommend that more attention be focused on the behavior of the animals themselves. By knowing more about how birds use their habitats, the ecologist can make better decisions about which habitat variables to measure.

ASSESSING BIRD HABITATS: A SYNOPSIS AND CRITIQUE

The usual way to examine the relationship between birds and their habitats has been to select a set of habitat characteristics and to relate these, frequently with the use of multivariate techniques, to the presence of bird species in those habitats. The habitat variables to be measured are often chosen rather arbitrarily, albeit based on the investigator's biological intuition as to what might or should be important to the birds.

The variables chosen often include some measure of plant species composition (usually the number of tree species) and several features that describe vegetation structure (often deciduous vs. coniferous foliage, tree size classes, canopy height, percent canopy cover, percent ground cover, etc.). Such measurements are either made 1) systematically through a study plot and then related to the avifaunal composition of that area (e.g. MacArthur and MacArthur 1961, James and Shugart 1970, Willson 1974, Titterington et al. 1979), or 2) on the territories of individual birds (e.g. James 1971, Whitmore 1975, 1977, Smith 1977). For the latter, the standard procedure has been to choose a song perch or nest site as the center of a 0.04 ha circle (11.3 m in radius) in which the habitat is then measured. One such circle is taken per territory, and a number of territories of each species are measured. The data so obtained are considered to characterize the places where the birds live, and have led to biologically meaningful correlations or ordinations (e.g. James 1971, Whitmore 1975, 1977, Smith 1977). Furthermore, with appropriate statistical techniques (see other papers in these proceedings) the habitat variables that are best correlated with the presence of a particular species can be identified.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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Putting aside for a moment the problems of arbitrarily chosen variables, there are a number of difficulties with these sampling techniques. For instance, since an area of 0.04 ha represents only a relatively small portion of the territories of most passerine birds, can habitat measurements made in a 22 m diameter circle around a single song\` perch adequately represent the habitat occupied by that bird? I contend, for reasons given below, that they may not. Also, how many territories must be measured to provide a statistically valid sample for representing the habitat occupied by the species? Most studies so far have taken measurements from an average of 10 to 20 territories per species, but none has yet evaluated how sufficient these sample sizes are.

Finally and more pertinent to the subject of this paper, these techniques provide little information, if any, on the reasons why the measured habitat variables might be important to the birds. Nor do they provide a basis for evaluating whether the most appropriate variables have been chosen in the first place. Thus, not only do the existing sampling methods need further development and testing, but the basic rationale for deciding what habitat components to measure in the first place requires re-evaluation.

HOW DO BIRDS USE THEIR HABITATS?

What then should we measure? What habitat variables are important to birds? To answer such questions, it is necessary to understand how birds utilize their habitats and what habitat components ultimately influence the survivorship and reproductive success of these birds. Although such information must eventually come from intensive population studies, considerable insight can be obtained from detailed observations of birds in their habitats.

By occupying a particular habitat, birds gain more than just a place to live (Hilden 1965). They obtain places to hide from predators, to escape vagaries of weather, to display, roost, nest and forage. The relative importance of these various functions differs from species to species and habitat to habitat. For example, suitable nest sites may be particularly important for desert birds (Tomoff 1974) or for cavity-nesters whose presence, abundance and reproductive success in a habitat will be determined in large part by the availability of suitable nesting sites (Conner 1978).

Perhaps the way in which habitats are used most intensively and extensively by birds, especially those inhabiting forests, is for foraging. With a relatively large proportion of their daily activities spent searching for food, birds move frequently from place to place and constantly scan plant surfaces, including tops and bottoms of leaves, twigs, branches and tree boles, for prey. Many of these birds move long distances during each foraging bout and at least in temperate forests, range widely from the forest floor to the upper parts of the canopy.[3]

To illustrate how observations on bird foraging behavior can provide information about what habitat variables might be important, I summarize here briefly some results from a study of birds in the Hubbard Brook Experimental Forest, West Thornton, N.H. The methods and analytical procedures have been described in detail by Holmes et al. (1979a). Basically, data were collected on the microhabitat use by birds foraging in this northern hardwoods forest during the breeding season, late May through mid July 1974-1976. Information was recorded on the height of foraging, the tree species on which foraging occurred, substrates to which foraging maneuvers were directed, and the kinds of foraging maneuvers employed. For purposes here, only the 11 bird species that forage primarily among the foliage of the forest canopy and the 20 appropriate foraging-related characters (table 1; Holmes et al. 1979a) are considered. The 20 x 11 "species" matrix (Q-technique, Sneath and Sokal 1973) was used to calculate the Euclidean distances between all combinations of the 11 species in the multi-dimensional space defined by the 20 foraging characters. This distance matrix was then subjected to hierarchical cluster analysis for purposes of illustrating species relationships (fig. 1). The transposed 11 x 20 'character' matrix (Q-technique, Sneath and Sokal 1973) was used for a varimax rotated factor analysis, as described by Holmes et al. (1979a).

The dendrogram in figure 1 groups the 11 bird species on the basis of their similarities or differences in microhabitat use/foraging behavior. There are clearly two major groups of foliage-foraging species in this community, each with two to several subgroupings. The relative importance of the characters that account for this pattern can be determined from the factor analysis, which weights the variables by their relative contributions to the total community pattern and reduces a large number of variables to a smaller number of identifiable factors (\`Cooley and Lohnes 1971, Bhattacharyya 1981). In this case, the first four factors account for 79% of the community variance (table 1), and illustrate how the birds differentially utilize foraging location, substrate and tree species. Thus, factor I largely accounts for the first major subdivision in the dendrogram. It separates those species that primarily hover for prey on leaves, hawk insects from the air and associate their

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[3] Holmes, R.T., unpublished data on file, Dartmouth College.

Table 1. The rotated factor pattern showing the most heavily weighted factors, either positive or negative, for each of 20 foraging characters (see Holmes et al. 1979a for further details).

Factors	I	II	III	IV
Eigen roots	7.24	4.27	2.47	1.71
Factor contribution to community variance (%)	36.22	21.36	12.39	8.56
Cumulative %	36.22	57.58	69.97	78.53
1 Hover leaf	0.889			
2 Glean leaf		0.728		
3 Hover branch				
4 Glean branch	-0.673			
5 Hover twig				-0.951
6 Glean twig	-0.929			
7 Hawk (air)	0.589			
8 Hover trunk		0.806		
9 Glean trunk	-0.805			
10 Proximal		0.946		
11 Distal		-0.971		
12 Beech	0.792			
13 Maple	0.743			
14 Birch	-0.920			
15 Ash	-0.499			
16 Shrub	0.799			
17 Conifer			-0.809	
18 Height (x)		-0.616		
19 Height SD			0.893	
20 Body size				

foraging with sugar maple (Acer saccharum) and beech (Fagus grandifolia) from those that glean prey, largely from twigs, branches and boles of trees and often forage on yellow birch (Betula allegheniensis) and white ash (Fraxinus americanus). The other factors illustrate further how species differently utilize the foraging environment by segregating those that glean prey from leaves, hover at tree boles and forage primarily in the inner (proximal) portions of the trees from those that forage distally along the branches, usually high in the canopy.

The finding that these birds are differentially using tree species and foraging substrates suggests that they are responding to, or are influenced in some way by, these habitat components. Indeed, it is very likely that these elements are closely linked, in that different kinds of foraging behavior may be required to exploit prey occurring on particular types of substrates which may vary in color, texture or frequency on different species of trees. This is supported by a more detailed study of bird foraging behavior which indicates that these insectivorous birds in the northern hardwood forests at Hubbard Brook have distinct preferences and/or aversions for certain species of trees while foraging (Holmes and Robinson 1981). This is attributed at least in part to differences among the tree species in arthropod abundances and in foliage arrangements that influence how birds search for and capture prey from plant surfaces. To determine the former, we utilized detailed information on insect abundances obtained from an intensive sampling of bird food resources (Holmes and Robinson 1981, Holmes et al. 1979b). For the latter, we found that bird species which typically glean arthropods have the strongest tree species preferences, in this case for yellow birch and for conifers (Holmes and Robinson 1981). On these plants, the leaves are arranged close to the branches so that a standing bird can reach prey situated on leaf surfaces. In contrast, in maple or beech, leaves are arranged either on flat sprays or at the ends of long petioles, and birds must fly and snatch their prey or hover for them at leaf surfaces. In addition, there is

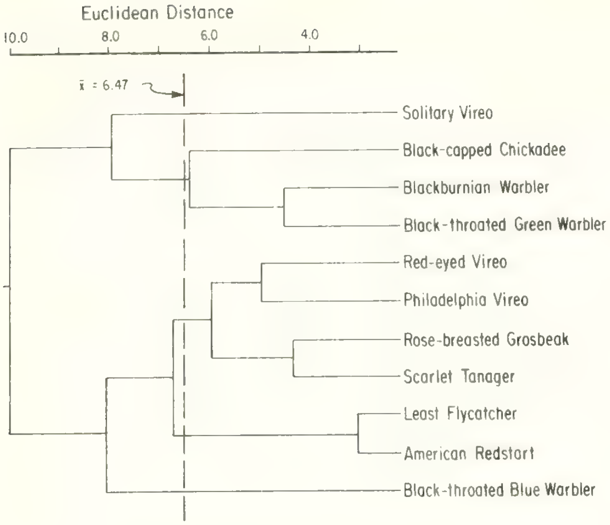

Figure 1. Dendrogram indicating the similarities and differences in microhabitat use among the 11 bird species at Hubbard Brook that forage for arthropod prey among foliage (for detail of technique, see text and Holmes et al. 1979a).

preliminary evidence that abundance and distribution of some of these bird species may be linked to particular tree species or at least to trees with similar physiognomic characteristics (Holmes and Robinson 1981).

The important point here is that observation of foraging birds has led to the realization that different species of broad-leaved trees in a primarily deciduous forest can be important habitat components. Although the potential importance of deciduous vs. coniferous foliage has been previously recognized (Balda 1969, Franzreb 1978) and occasionally incorporated into habitat analyses (e.g. Titterington et al. 1979), most studies of bird habitats have not taken into account the occurrence of particular tree species. It must be realized, however, that even if tree species were to be included and if correlations were found, there would still be no way of understanding why these tree species are important without detailed observations of what the birds were doing in the different tree species and without measurements of the resources available there.

CONCLUSIONS

A thorough knowledge of the natural history of bird species and their habitat requisites is essential for understanding the relations between birds and their habitats and for determining which habitat components are important to birds. To elucidate further the causal links between birds and their habitats, however, will require comparisons of behavior and habitat responses of the same bird species in habitats that differ in particular ways or that have been manipulated in a manner that will test the importance of some specific habitat parameter(s). Only through such carefully planned observations and experiments can knowledge be obtained that will allow us eventually to predict from habitat data which bird species will occur or not occur in particular habitats. Such a goal is needed if habitats are to be managed scientifically.

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APPLIED ASPECTS OF CHOOSING VARIABLES IN STUDIES OF BIRD HABITATS[1]

Robert C. Whitmore[2]

Abstract.--This paper considers the applied aspects of choosing and using habitat variables; aspects that deal with management decisions rather than evolutionary events that shaped observed community patterns. Vegetation structure is one of the central parameters used in the explanation of observed habitat use patterns of birds. When choosing variables one should consider the range of habitats being studied, the nature of the bird species, the practicality of measurement, the time (cost) needed to measure and the biological importance of each variable. Once the variables are chosen, experimental designs by Martinka (1972) and Whitmore (1981) could be used to gather information needed in making management decisions. The designs basically involve comparing bird territories with adjacent areas that are not occupied (nonterritories).

Key words: Blue grouse; discriminant analysis; grasshopper sparrow; habitat management; variables.

INTRODUCTION

Criteria for determining which habitat variables to measure generally fall into two broad categories, theoretical considerations and applied considerations. The former deal with studies that ask why certain species of birds inhabit a given locale and what events shape this process, while the latter deal primarily with management decisions. The objective of this paper is to discuss applied aspects of the question.

When trying to quantify observed habitat use patterns of birds, variables most often measured reflect vegetation structure. There are two readily apparent reasons for this. First, vegetation structure is a central factor determining the habitat that a bird selects (fig. 1) and, although only a proximate factor (Hilden 1965), does evoke the settling response of a bird arriving in spring. Second, between-site differences in vegetation structure often are obvious and while data sets may be voluminous they are relatively easy and inexpensive to obtain, especially when compared to other parameters such as food availability, microclimate and biological interactions. With increasing use of multivariate statistics in habitat studies, the number and complexity of variables measured have increased (James 1971, Anderson and Shugart 1974, Whitmore 1975, 1977). Moreover, it is likely that the number of these types of studies will increase and, in fact, the call for more has already gone out: "Detailed investigation of the relationships among numerous habitat variables and bird populations...should be encouraged. Such investigations will likely provide widely applicable results in a minimum of time" (Verner 1975).

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[1] Paper No. 1643 of the West Virginia University Agriculture and Forestry Experiment Station. Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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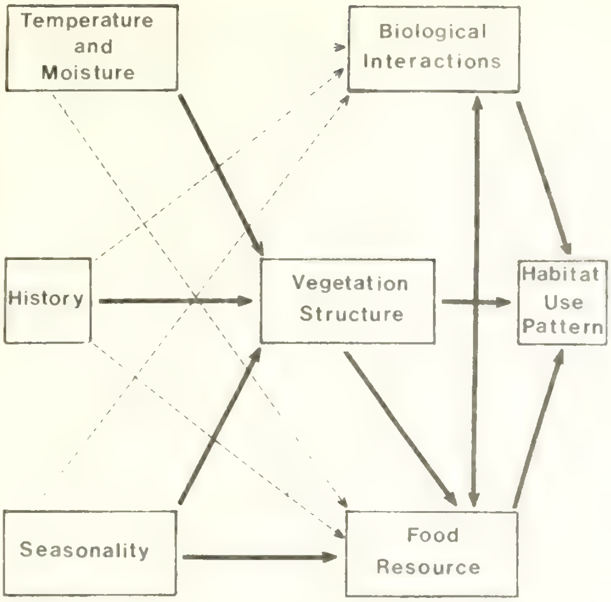

Figure 1. Schematic representation of the relationship between vegetation structure, other variables and observed habitat use patterns in birds. Dashed lines represent minor effects while solid lines represent major effects. Adapted from Karr (1980).

Although the ecologist may not be seeing or measuring what the bird is actually selecting (i.e., "the ecologist may be recognizing distinct habitats or positions along environmental gradients, but the bird species present may not be capable of the same distinctions or their distinctions may not be equivalent to those of the observer", Whitmore 1977), detailed multivariate analysis of species distributions along complex habitat gradients may have predictive value in determining which species will occupy a given site, and may be useful in making management decisions (James 1971, Martinka 1972, Whitmore 1981). However, as pointed out in numerous studies, the choices and number of variables (James 1971) as well as time of year in which they were measured (Whitmore 1979) affects results. Therefore, any multivariate study is only as good as the input variables. The following sections of this paper will first examine criteria for selecting variables and then give an example as to how they might be used in an applied situation.

CRITERIA FOR SELECTING VARIABLES

The plethora of avian habitat studies can be placed along a continuum of "quantitativeness" ranging from subjective, visual analysis (extensive), such as the Missouri Plan for habitat evaluation, to microhabitat analysis (intensive) which may be as detailed as counting the number of grass stems in a 5 ha field. As an example of an extremely extensive methodology I am reminded of the waterfowl manager who developed a three category system for analyzing marsh vegetation: If a duck can swim through it in a straight line--open; weaving line--moderate; can't make it through--dense.[3] In the middle of the continuum of quantitativeness lies what I term "quick and dirty" methods of habitat analysis. One of the most widely used of such techniques was proposed by James and Shugart (1970) and has been used in a variety of studies (see Whitmore 1975, 1977). More detailed analysis, the intensive methods, can be seen in works of Cody (1968) and Wiens (1969) for their analyses of grassland habitats.

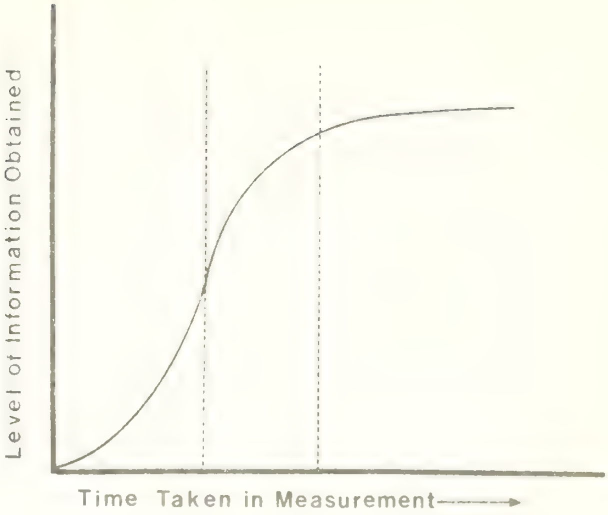

Figure 2. A curve representing the relationship between the level of information obtained and the time taken in measurement. Dashed zone indicates an optimal area where the ratio produces the most benefit per unit expended.

A fundamental criterion for picking a sampling technique is the time needed and relative cost of each method. When plotting the time taken in measurements versus the level of information obtained a Gaussian curve emerges (fig. 2). Somewhere in the middle of the curve is a "zone of optimality" where a maximum return in information for amount of time (money) expended is obtained. An effective sampling scheme should fall within this zone. For the scope of many studies the James and Shugart (1970) technique fits the bill. It remains for others to develop techniques that will shift the curve to the left on the abscissa thereby increasing the ratio of information/time spent.

The nature of variables measured depend on the range of habitats being considered. Quantifying habitat use of birds in habitats ranging from grassland to forest may require less intensive variables than are necessary to separate four Panamanian forest plots. Another consideration is what kind of species are you dealing with? Would variables used to quantify habitats of an acorn woodpecker (Melanerpes formicivorous) also be appropriate for a grasshopper sparrow (Ammodramus savannarum)?

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[3] Personal communication with E.D. Michael, Professor, West Virginia University.

Some practical aspects when deciding which variables to pick might fall into three general categories. First, variables should be measurable to the desired level of precision. Second, variables should be biologically meaningful. For example, it may be possible to measure tree roots to 60 cm away from the trunk below the surface of the ground, but what possible meaning could this have to a canopy foraging bird such as a cerulean warbler (Dendroica cerulea)? Third, variables should be relevant to the species in question. Would percent grass cover or the ratio of grasses to forbs be important to a bark forager such as a brown creeper (Certhia familiaris)?

As a preface to the next section I would like to make two comments that seem to have a bearing on many of the papers in these proceedings. First, we scientists are often guilty of measuring everything there is to measure, trusting stepwise discriminant analysis or some other technique to sort things out, simply because we don't know what is important. This may be viewed simply as a substitutive for thinking. And second, if you miss the key parameters you can go out and measure everything else, use the most sophisticated multivariate techniques and still have nothing of biological importance. However, if one is careful in picking variables and follows, at least generally, the concepts listed above, then multivariate statistics may be useful in sorting out habitats and making management decisions.

USING MULTIVARIATE STATISTICS IN WILDLIFE MANAGEMENT

Assuming correct variables are measured, this section deals with application of multi-variable data sets to wildlife management. Standard management questions might include:

1. What effect will habitat alteration have on the bird species in question (BSIQ)?
2. What structural characteristics are found in habitat type A but not in type B that allow the BSIQ to live in the former but not the latter?
3. How can I make habitat type B suitable for the BSIQ?
4. How can I get more of the BSIQ into type A?
5. Can I introduce the BSIQ into habitat type C?

From reading papers in the Journal of Wildlife Management it is apparent that multivariate statistics as a tool in making management decisions have not had widespread use. The only multivariate paper of interest that I could find in recent volumes of the Journal of Wildlife Management presented a technique for habitat analysis that I feel has broad application in wildlife management. However, it has apparently been overlooked. Martinka (1972) published a study comparing habitats of blue grouse (Dendragapus obscurus) with surrounding habitat that appeared similar but did not have blue grouse using it. He termed the latter sites "nonterritories." This type of analysis, territory vs. nonterritory, seems appropriate in addressing several questions listed above. Basically, Martinka found that by using discriminant analysis he could correctly classify 96% of his plots as either territories or nonterritories and by so doing develop a model for management recommendations.

This same line of reasoning may be of fundamental use in documenting avian habitat use in general. Most studies are designed to compare different bird species or different communities. Perhaps it would be more fruitful to look at a single species, comparing sites in which it is found with similar habitat where it is not found. As an example of this method I summarize a paper on grasshopper sparrows (Whitmore 1981). This species is a common breeder on reclaimed surface mine grasslands in northern West Virginia, yet not all sites have grasshopper sparrows and on those that do it is rare for the entire area to be used. Questions asked were 1) are there vegetational structure characteristics that are identifiably different between used and unused areas, and 2) if there are, can the unused areas be managed to make them usable? On one reclaimed site in Preston County, West Virginia all grasshopper sparrow territories were located and mapped using the territory flush technique (Wiens 1969). Once mapped, vegetation structure variables were measured in each territory. All areas on the same mine that were not used by grasshopper sparrows (nonterritories) were located and sampled. By using stepwise discriminant analysis it was found that territories could be separated from nonterritories with 100% accuracy on a vegetation density gradient. Nonterritories had significantly greater ($P < 0.01$) values for most grass, shrub and litter cover variables and significantly lower ($P < 0.01$) percent bare ground. A change in the habitat from unusable to usuable could be manifested by any of a variety of range management techniques that would reduce vegetation density and litter build up; the easiest being fire. Manipulation experiments are currently being designed in an attempt to shift unused habitat to usable.

Further extension of the above two examples may be necessary to fit different species or groups of species. However, the basic concept could be used in a variety of wildlife studies ranging over many habitat types.

SUMMARY

Many studies presented in the current body of literature are based on a set of variables that seem to be picked with little regard for the habitats or species in question and more often than not are based on either convenience or "what someone else has done." This paper presents a set of ideas that should be considered before initiating a bird habitat study. Two examples of an experimental design based on vegetation analysis of territories vs. nonterritories, one with a game bird the other with a songbird, show great potential for future use in making management decisions. Scientists should remember that the choice of vegetation variables, the number of variables, and the time required for measurement can greatly affect results in a multivariate study. Perhaps the greatest amount of time should be spent in the design and variable selection stages of the experiment rather than in the collection of data.

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DISCUSSION

JAMES DUNN: How did you decide on the locations of the non-territories?

BOB WHITMORE: We had the entire surface mine mapped as to territory location. All areas that did not have territories were sampled, subject to the constraint that an entire 50 m radius circle would fit within it.

JIM WOEHR: Do you agree that vegetation patchiness is an important habitat variable, and if so, how should we measure it and how can we statistically test for differences in patchiness?

BOB WHITMORE: I agree it is important, but I do not have a real handle on how to measure it.

JIM WOEHR: In comparing territories with non-territories, do you think it is critical to study a habitat over several years to look at fluctuations in bird density in different habitats? It seems to me that the "best" habitat will always have more birds, whereas marginal habitats will have fewer birds, or none at all, in years of low populations.

BOB WHITMORE: I totally agree that in most natural systems yearly changes in environmental factors such as climate will affect avian densities and habitat use patterns, often forcing birds into "suboptimal" habitats. Although it is difficult to determine quantitatively, I feel that the strip-mine birds, as yet, are not habitat limited and, therefore, are taking the best available. Newly reclaimed surface mine habitat is being created faster than the birds are capable of using it. We definitely need some bad years to study.

TECHNIQUES FOR SAMPLING AVIAN HABITATS[1]

Barry R. Noon[2]

Abstract.--Standardized methodologies for the sampling of bird-related vegetation structure in forest and non-forest habitats are proposed. For forest habitats, the methodology is based largely on techniques proposed by James and Shugart (1970). For non-forest habitats, the methodology is a synthesis of many previously published techniques, particularly those of Wiens (1969). For each habitat type a detailed sampling protocol and sample field data sheet are provided. In addition, statistical and biological considerations for the location of sampling points are discussed. The paper ends with an argument in favor of standardized methods of sampling avian habitats.

Key words: Avian; habitat structure; sampling techniques; standardized procedures.

INTRODUCTION

There are two common goals when sampling avian habitat structure. The first is to measure features of the habitat that will allow an accurate determination of the species' habitat requirements. Habitat parameters believed to be at least proximally related to a species' survivorship and reproductive success in that habitat are selected for measurement. The second is the ability to make accurate predictions of a species' response to habitat change and to anticipate possible detrimental effects to a species population from various land-use practices. This second goal is contingent upon having achieved the first.

To date, there have been a variety of approaches to describing the habitat associations of bird species (Niemi and Pfannmuler 1979). These include the non-quantitative successional stage (Kendeigh 1945, Johnson and Odum 1956, Martin 1960, Haapanen 1965, Holt 1974) and life form (Thomas et al. 1975, 1976) approaches, as well as quantitative approaches based on statistically defined species-habitat associations (e.g., Rotenberry and Wiens 1978, Pfannmuller 1979) or the multidimensional habitat-niche approach adopted from Hutchinson (1957). The statistically based, quantitative approaches are currently favored because they are generally less subjective and yield more information on specific niche requirements than do non-quantitative approaches.

A holistic, community based approach to species-habitat associations has been outlined by Niemi and Pfannmuller (1979). The procedure is based on a cluster algorithm which groups avian communities, representing various points along a habitat gradient, into hierarchial clusters on the basis of their similarity in species composition. The researcher investigates whether the groups formed by the clustering algorithm(s) suggest any structural features of the habitat gradient recognized as important by the birds. The same community census data can be subjected to an inverse clustering algorithm which groups together bird species that show similar distributions across the habitat gradient (Pfannmuller 1979).

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

[2] Research Biologist, Migratory Bird and Habitat Research Laboratory, U.S. Fish and Wildlife Service, Laurel MD 20811.

The distribution of species associations and the community clusters may yield insights into the habitat requirements of individual species and also indicate which habitats are recognized as distinct types.

The avian community approach does not yield information on specific habitat niche requirements of individual species. However, it is a valuable preliminary to more detailed niche analysis because it accurately delimits the range of habitats to be sampled for a particular species or species association.

To clarify the relationship between birds and habitat structure, we must develop techniques of habitat measurement which fulfill the following criteria:[3]

1. Yield efficient, precise, and accurate estimates of the habitat parameters of interest.
2. Yield data amenable to various statistical tests, especially in multivariate analyses on which predictive models would subsequently be based.
3. Quantify attributes of the habitat that are biologically relevant to the species (and biologically interpretable) and that can be unambiguously communicated to other researchers.
4. Yield data whose predictive capabilities can be tested by simulated tests.
5. Are applicable in different structural habitat types.

The sampling protocol that follows is based on a multivariate approach to habitat selection, specifically on the niche concept as formalized by Hutchinson (1957). The rationale for employing these techniques is the belief that a species' response to habitat structure is not univariate. That is, the suitability of a habitat patch to an individual bird is a function of several interrelated habitat parameters whose combined effect (in a mathematical sense) determines the habitat's suitability.

When initiating a habitat-based niche analysis of one or more species, three major aspects of the experimental design must be resolved before sampling begins. I will address each of these below.

How Finely Should Habitat Be Measured?

Obviously, the habitat structure must be measured in enough detail so that factors believed important to the species being studied are accurately estimated. In addition, habitat structure should be measured so as to bring into focus differences that may allow two similar bird species to coexist. These data will also give valuable insights into community organization.

As a general rule, the more apparently homogeneous the habitat, the finer it will need to be sampled in order to detect its inherent heterogeneity. Thus, grassland habitats require sampling vegetation structure at a much finer level than would forest habitats (cf. Wiens 1969 with Whitmore 1975).

Often the researcher is uncertain how finely species are discriminating habitat and, as a consequence, feels the need to sample both micro- and macrohabitat gradients. Macrohabitat descriptions require sampling a relatively large area, while sampling microhabitat gradients over the same area would result in prohibitive time constraints. A workable solution is to use nested samples with microhabitat variables estimated from sampling areas contained within the larger sampling units used to estimate macrohabitat variables. Titterington et al. (1979) provides a good example of the use of nested vegetation sampling plots in the study of avian populations.

How Many Samples Should Be Taken?

This topic is covered in more detail by Johnson (1981); however, a brief point follows. A sampling criterion such as being within 10 percent of the population mean 90 percent of the time should be established for each habitat parameter estimated. Sample size formulas to meet these and other criteria are given in Cochran (1963) and Steel and Torrie (1960). Unfortunately, for some parameters of interest the appropriate sample size to meet these criteria is impossible to attain (Noon, unpublished data). This is particularly true for habitat variables or gradients that are very patchily distributed in the study area (e.g., the percent of coniferous vegetation in different vertical strata in a primarily deciduous woods). For example, using the above criteria, a mature deciduous forest plot in New York State (Noon 1979) required over 100, 0.04 ha circular plots to estimate most structural habitat parameters. Changing the criteria so as to be within 10 percent of the mean 80 percent of the time lowered the requisite sample size for the same variables to approximately 60 circular plots.

Where Should Samples Be Taken?

A major assumption of most statistical models is that the statistics themselves have been estimated from a random sample of the population under study. When estimating structural parameters of the vegetation relative to the bird community, stratified random sampling may be more appropriate than pure random sampling. Stratification will result in a more uniform sampling of the study area. I suggest that the stratification be based on the following criteria:

1. Along obvious lines of habitat

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[3] Personal communication with Frances James, Associate Professor, Department of Biological Science, Florida State University.

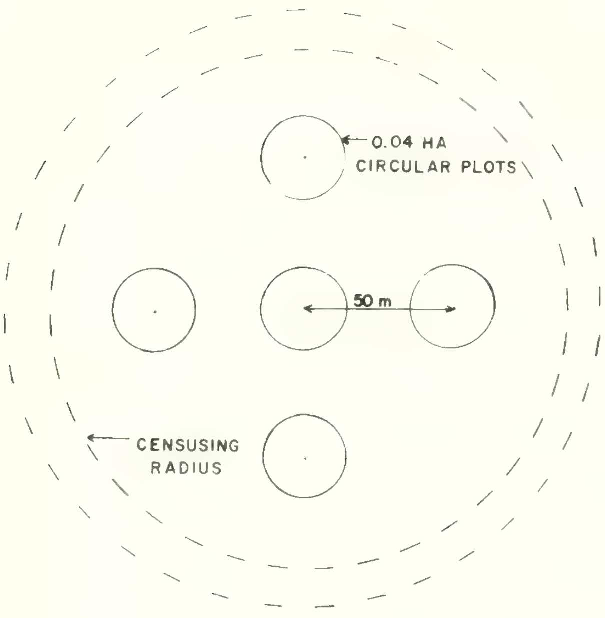

Figure 1. Point-count census technique with variable censusing radius. Five, 0.04-ha circular plots for sampling vegetation structure are clustered about the censusing point.

heterogeneity within the study area. It is very important that patches of structurally distinct habitat be represented in data from which estimates of available habitat are made.

2. By the location of individual birds in the habitat; that is, let the bird define the sampling location.

The importance of bird-defined sampling locations is clarified by examining how easily erroneous inferences about a species' habitat requirements arise from improper sampling. I will illustrate the problem with bird census data collected with the point count technique (Ferry and Frochot 1970) and habitat data subsequently gathered from 0.04-ha (0.1 acre) circular plots (James and Shugart 1970) centered around the censusing point.

Figure 1 illustrates a sampling design with five, 0.04-ha circles clustered about the censusing point. A hypothetical study using this experimental design would conduct many point-counts along a habitat gradient and associate all the species recorded at a particular censusing location with the mean habitat vector (averaged across the five circles) at that location. A two-group discriminant function analysis may then be conducted, for each species, to distinguish points where the species was found from points where it was not detected. Discrimination of these "present" and "absent" groups would be interpreted in terms of differences in habitat structure.

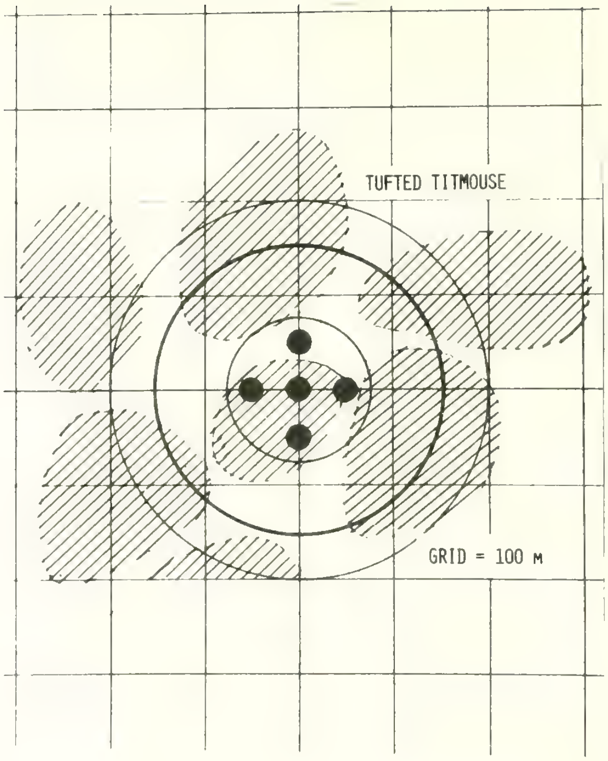

Figure 2. As in fig. 1 but with actual tufted titmouse territories (determined by territory mapping) detectable from the point-center positioned relative to the vegetation samples.

Figure 2 illustrates the actual location of tufted titmouse territories around one of these census points. Note that habitat data from non-utilized areas are associated with the species. If the habitat sampled from non-utilized areas is substantially different from the utilized areas, then it will be quite difficult to discern the true habitat preferences of a species with this experimental design. The problem is not unique to this sampling situation but may arise anytime habitat data associated with a particular individual represent areas not actually utilized by that individual.

METHODS

I have outlined a sampling methodology that combines random, or statified random, sampling with bird defined sampling locations as follows (see figs. 3 and 4): 1) Samples of vegetation structure are taken at randomly selected locations within the study plot boundaries. Vegetational characteristics of individual territories are determined by superimposing a map of the territory boundaries over a map of the numbered sampling sites and summing the data from all sample sites included within the boundaries (Wiens 1969). Only samples falling totally within territory boundaries are assigned to that species. 2) Territories that by chance were not sampled

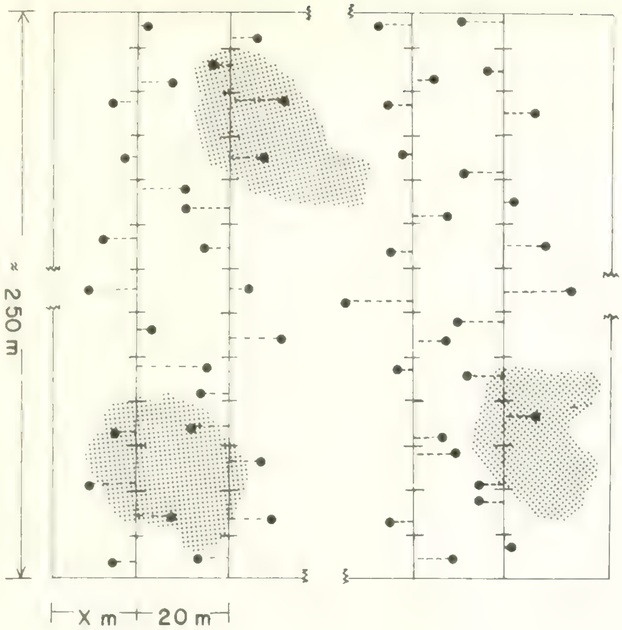

Figure 3. Line transect system with randomly located sampling points indicated. Territories are superimposed over sample locations.

are sampled in some random fashion.

Given sufficient data, this sampling scheme allows direct comparison between species' structural habitats as well as a comparison of each species against a random sample of the available habitat. The sampling protocol is amenable to studies in both non-forest (≤ 25 percent cover by trees) and forest habitats. I suggest that non-forest habitats be sampled by line transect methods and forest habitats by a modification of the James-Shugart (1970) 0.04-ha circular plot technique. Transects should be placed across contour lines (Oosting 1956), and evenly spaced across the study plot with the location of the initial transect line determined by some random process (fig. 3). For forest habitats, sampling points can be determined by a random (or stratified random) selection of grid points used in the territory mapping procedure (fig. 4).

Sampling Protocol

Non-forest Habitats

Avian habitat studies in "non-forest" environments (≤ 25 percent cover by trees) have used primarily transect sampling procedures to establish sampling locations. Along the transect, or at randomly selected points, vegetation structure has been estimated by fixed quadrat, line intercept, or point-centered quarter techniques (refer to Smith 1974 for a general description of these procedures). I propose a sampling protocol that combines line-intercept and point-centered quarter techniques. In developing this protocol I have borrowed extensively from the work of others, particularly Wiens (1969).

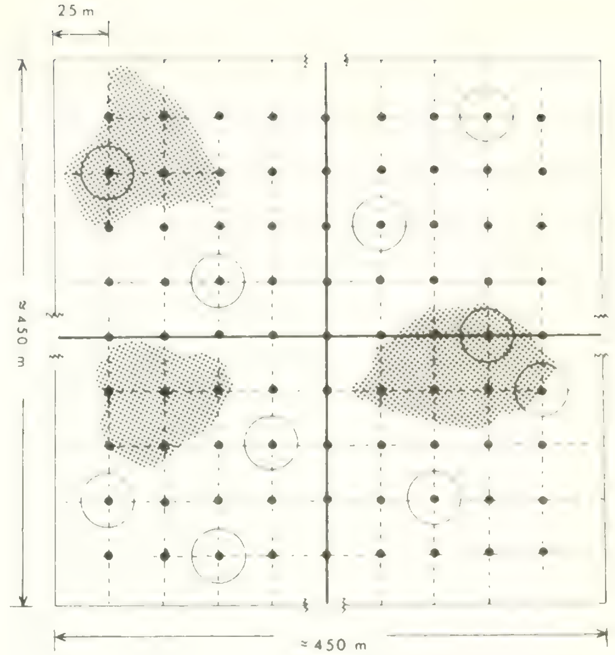

Figure 4. Areal plot system with randomly located 0.04-ha circular plots indicated. Territories are superimposed over sample locations. The 25-m grid system illustrated here would only be necessary in very closed habitats.

Line-intercept Variables. The line is considered to be a belt 1 cm wide running along one side of the transect. The transect is divided (stratified) into 10-m intervals. Within each interval the distance on the transect line interrupted by specific life forms or habitat features is recorded (appendix IA).

For shrub and tree life forms, coverage is estimated by the downward vertical projection of their foliage lying above the line. Within each 10-m segment the minimum total amount of coverage summed over all habitat features is equal to the length of that segment; however, total coverage is usually higher. Data collected in this way allow calculation of the frequency, density, and dominance of each habitat feature (Smith 1974).

If the ground-level vegetation is not arrayed as discrete patches then line-intercept techniques are very difficult to use. When the ground cover is an intricate mosaic, line-intercept techniques should be replaced by point-intercept methods. The procedure is to uniformly select numerous points within each 10-m interval and record the presence and absence of specific ground cover life forms intercepted at these points.

Statistical treatment of the results and cautionary notes on methods of point sampling are found in Goodall (1952).

Point-quarter Variables. Each 10-m interval along the transect will correspond to a sampling unit. Within each interval the sampling point is determined by selecting three random digits to indicate 1) the linear distance in meters along the transect interval given by the first digit, 2) the side of the line to be sampled (odd digit = left; even digit = right) given by the second digit, and 3) the number of 0.5-m intervals to be marked off perpendicular to the transect given by the third digit. At the sampling point, quarters are established by placing two 1-m sticks on top of each other oriented in the cardinal directions to form a '+'. Within each quarter the following variables are estimated:

A. Species, distance to, and height of the nearest shrub (woody vegetation > 1 m tall and < 3 cm dbh).
B. Species, distance to, dbh, and height of the nearest sapling (3 cm $\leq$ dbh < 8 cm) and tree ($\geq$ 8 cm dbh).
C. Vertical vegetation density. At each of the four ends of the meter sticks, vertically lower into the vegetation a 1-cm diameter rod graduated into the following intervals: 0-0.3 m, 0.3-1 m, and 1-2 m. Vertical vegetation density is estimated by recording the number of contacts of vegetation falling within each interval as well as visually estimating the number of contacts from 2-9 m and > 9 m.
D. "Effective vegetation height". At the approximate intersection point of the two meter sticks record "effective vegetation height" as detailed by Wiens (1969).

Methods to calculate density, dominance, and frequency estimates from point-quarter data are given in Smith (1974). A sample field data sheet is given in appendix II.

Forest Habitats

The sampling protocol for forest habitats (> 25 percent cover by trees) is based on the James and Shugart (1970) 0.04-ha (0.1 acre) circular plot techniques. I have modified the techniques to include additional data and to clarify existing ambiguities (cf. James 1978); however, the core of the technique remains unaltered. A sample field data sheet for recording the estimates outlined below is given in appendix III.

The following habitat features are measured within the 0.04-ha (radius = 11.3 m) circle:

1. The diameter at breast height (dbh), 1.3 m above the ground, of all saplings and all standing trees. The dbh values will be recorded by tree species within nine size classes (appendix IB). Standing, dead trees are recorded separately by size class. The size classes are almost identical to those proposed by James and Shugart (rounded to nearest cm) but with the addition of a smaller dbh size class, S (sapling: 3-8 cm dbh).

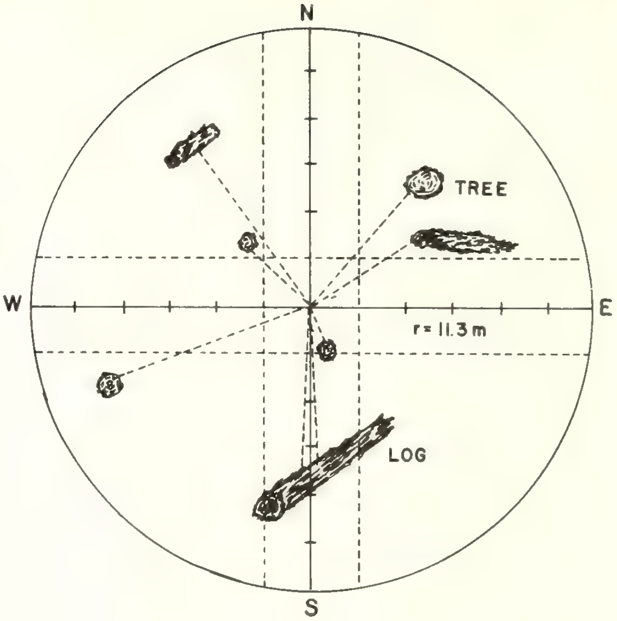

Figure 5. Circular plot (r = 11.3 m) used to estimate vegetation structure in forest habitats. Rectangular plots used to estimate shrub density, transects establishing quarters, point-quarter tree and log variables, and sample points for estimating canopy and ground cover are all indicated.

2. Shrub density at breast height is estimated along two transects running in the cardinal directions and centered within the 0.04-ha circle (fig. 5). The observer proceeds along the transect lines counting the number of woody stems < 3 cm dbh intersected with his body and outstretched arms at breast height. Counted stems only include the main stem and those stems branching from the main stem below breast height. The total number of contacts made in two transects (each 22.6 m long) times 125 is used to give an estimate of the number of shrub stems per ha. The contribution of deciduous and coniferous shrubs is recorded separately.
3. Canopy cover and ground cover are estimated by sighting through an ocular tube, made from a cardboard cylinder with cross hairs at one end. The observer walks along the transect lines used to estimate shrub density sighting up to the canopy and recording a total of 20 (10 each transect) plus or minus readings indicating the presence or absence,

respectively, of green vegetation at the intersection point of the cross hairs. Percent of the canopy cover contributed by coniferous foliage is recorded in addition to total canopy cover. Green vegetation within a meter of the ground is recorded in an identical manner except that the observer sights downward through the tube held at waist height (approximately 1 m above the ground). Canopy and ground cover are recorded as percents (i.e., number of hits/20 x 100).

4. A qualitative plant dispersion index is recorded for ground (0-1 m tall) and shrub (> 1 m tall and < 3 cm dbh) strata plants. The index is identical to that proposed by Emlen (1956). The categories are
   E - Even matrix (more or less randomly dispersed)
   I - Irregular or uneven (indistinct clumps)
   SC - Small clumps
   LC - Large clumps
   SR - Small distinct rows or hedges
   LR - Large distinct rows or strips.
5. Canopy height should express the average height (m) of the canopy within the 0.04-ha circle. The observer should make several measurements (with a clinometer, range finder, Abney level, or similar instrument), average these measurements, and record this average. Also, the maximum and minimum estimates of canopy height are recorded.
6. Slope is estimated with the aid of a clinometer. This estimate is the maximum slope within the circular plot.
7. Indices of tree and log dispersion are gathered from point-quarter techniques. The point is centered in the circle and the quarters are established by the transects used to estimate shrub density (fig. 5). Within each quarter the distance to, and dbh size-class of the nearest tree are recorded. In addition, the distance to, total length of, and dbh size-class of the largest (by diameter) fallen log (≥ 1.5 m in length and ≥ 8 cm dbh) are recorded (fig. 5). The dbh size-class of the log is determined by the maximum dbh attained throughout its length whether lying totally within the plot or not.
8. Understory foliage volume is estimated with a density board (Wight 1938, DeVos and Mosby 1969). The density board, or drop cloth, (fig. 6) is divided into four height intervals, 0-0.3 m, 0.3-1 m, 1-2 m, and 2-3 m, corresponding to low ground, high ground, and low and high shrub levels, respectively. Foliage volume contributed by the sapling level is indirectly assessed by the number of trees falling in dbh size-class S. The drop cloth is placed at each of the four points where the transect lines intersect the edge of the circle. Four readings are made from the center of the circle (i.e., 11.3 m distance) sighting along each of the transects (i.e., N,S,E,W). The observer counts the number of squares within each height interval at least 50 percent obscured by foliage and records this number. To minimize parallax problems, foliage volume in the first two height intervals is estimated from a crouching position, and from a standing position for the upper two intervals. Problems may arise if dense, low vegetation lies within the immediate vicinity of the center of the circle (≤ 1.5 m). In this situation the observer should move to the side the minimum distance necessary to give an unobstructed view within the first 1.5 m.

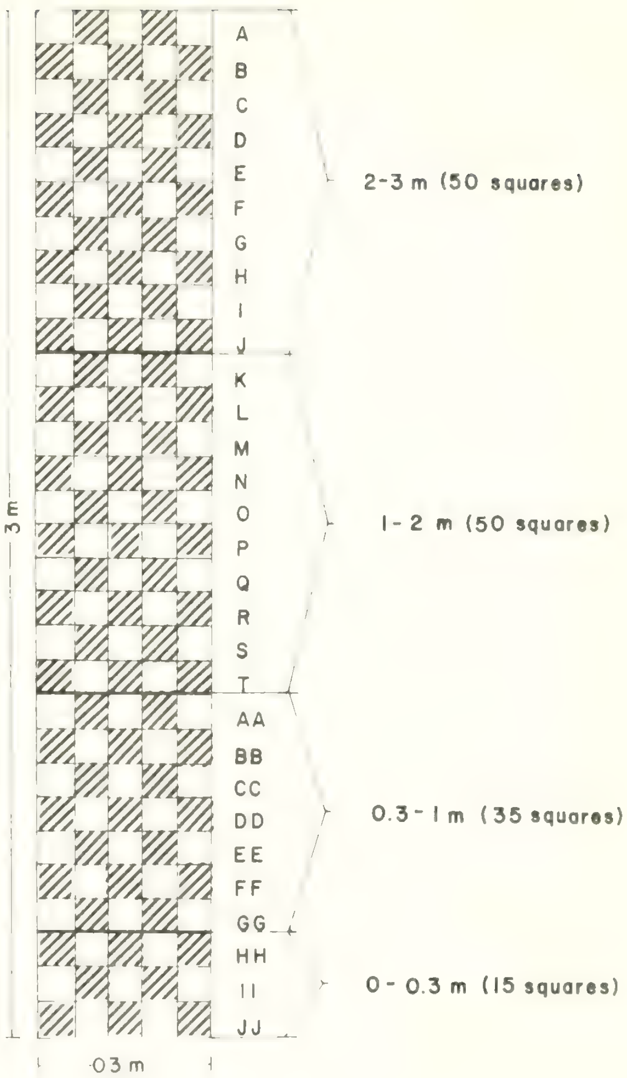

Figure 6. Density board ("drop cloth") used to estimate foliage volume from 0-3 m.

9. Dominant shrub species and ground cover (ground to 1 m tall) life forms are recorded in rank order with the most common species, or life form, listed first. The ranking is estimated only within the 0.04-ha circle. A list of ground cover life forms to discriminate is given in appendix IC.

Equipment needed for estimating density, basal area, and frequency of trees, canopy height, shrub density, and percent ground and canopy cover is given in James and Shugart (1970). Sapling trees are measured with a forester's diameter tape. Density boards (drop cloths) can be made from a variety of materials but those made with either oil cloth or vinyl prove to be both resilient and portable. The gradations are scored on the material with an indelible marking pen. The drop cloth is extended to its full height with the aid of a "telescoping" aluminum pole such as is used by painters and window washers. When not in use, the drop cloth may be rolled around the wooden dowel used to attach the top of the cloth to the aluminum pole.

DISCUSSION

Many of the papers presented in these proceedings have used a habitat sampling protocol similar to that outlined here and illustrate a variety of approaches to data analysis and interpretation. Additional sources of references are Anderson and Shugart 1974; Bertin 1977; Bourgeois 1977; Cody 1968, 1978; Cody and Walter 1976; Conner and Adkisson 1976; James 1971; Karr 1968, 1971, 1976; Karr and Roth 1971; Noon 1981; Noon and Able 1978; Rabe 1977; Rice 1978; Roth 1976; Smith 1977; Sturman 1968; Titterington et al. 1979; Whitmore 1975, 1977, 1979; and Wiens 1968, 1973, 1974.

Ecologically meaningful information may be derived from understory foliage volume and tree size-class data. Vertical foliage volume is directly estimated up to 3 m by the drop cloth. Further, indirect estimates of foliage volume may be extracted from dbh size-class data for specific species or types of trees (e.g., hardwoods and conifers; Harris et al. 1973, Weinstein[4], Smith[5]). This results from the predictable relationship between tree height and dbh for the lower size classes (S-C) of most species of trees (fig. 7; e.g., Curtis 1967; Schreuder and Hafley 1977). Coupling these two sources of information by tree species or tree type allows estimates of foliage volume by vertical strata.

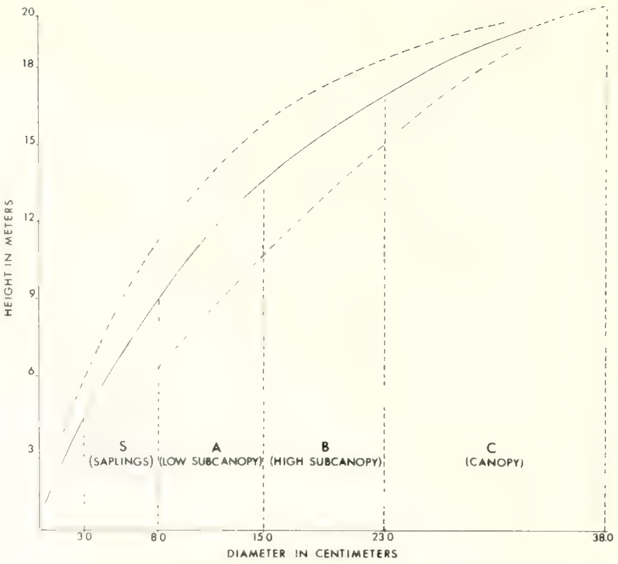

Figure 7. Regression of tree height on diameter at breast height (modified from Schreuder and Hafley 1977).

As an example, consider the data collected by the modified James-Shugart techniques outlined here. Estimates of foliage volume from the drop cloth are stratified as 0-.3 m (low ground), 0.3-1 m (high ground), 1-2 m (low shrub), 2-3 m (high shrub), and for the tree strata (fig. 7) as 4-9 m (saplings), 9-14 m (low subcanopy), 14-17 m (high subcanopy), and > 17 m (canopy). Estimates of foliage volume at different vertical strata allow calculation of total foliage volume as well as both vertical and horizontal foliage distribution and heterogeneity.

Several horizontal habitat heterogeneity indices have been proposed (Wiens 1974, Roth 1976, Anderson et al. 1979). However, the technique used by Anderson et al., based on the variance in foliage volume both within and across vertical strata, is most amenable to data of the type considered here. Insights into the relationship between total foliage volume and bird species abundance, and between vertical and horizontal foliage heterogeneity and bird species diversity may arise when detailed vegetation data are combined with information on the spatial distribution of birds in the habitat.

CONCLUDING REMARKS

The standardized procedures outlined above are not meant to be a constraint on additional or new ways of looking at avian habitat structure. However, I believe that several points can be made in favor of some degree of standardization in methodology. First, standardized methods will clarify communication among researchers and avoid ambiguities in the interpretation of avian-habitat interrelations. Second, standardized data will allow researchers to address questions requiring comparable data sets. For example, two researchers who had studied the habitat relations of a species in different parts of its range could collaborate to examine the extent of geographical variation in habitat use by that species. The Breeding Bird Census data, with associated James-Shugart structural vegetation data, have already permitted geographical comparisons (Robbins 1978, Noon et al. 1980, James and Wamer, ms) because of standardization in sampling methodology. Finally, once researchers and land managers have reached a common interpretation of the habitat parameters, research findings can be more directly incorporated into land management practices for avian species.

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[4] Manuscript in preparation, D.A. Wienstein, Environmental Science Division, Oak Ridge National Laboratory.

[5] Personal communication with Thomas R. Smith, Environmental Science Division, Oak Ridge National Laboratory.

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Stanley Anderson, Deanna Dawson, Douglas Inkley, Frances James, and Chandler Robbins have contributed extensively to the ideas presented here. In addition many biologists at the Migratory Bird and Habitat Research Laboratory have field tested these techniques and offered valuable criticism. However, I did not always heed the advice of my colleagues and much of the methodology and emphasis on "important" variables reflects my personal biases.

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Appendix I

Life forms and habitat features

A. Life forms and habitat features to be discriminated as line-intercept variables.

Grasses - Narrow-leafed herbaceous plants

Forbs - Broad-leafed herbaceous plants

Woody ground cover - Woody vegetation < 1 m tall

Shrubs - Woody vegetation > 1 m tall and < 3 cm dbh

Saplings - Woody vegetation > 1 m tall and $3 \text{ cm} \leq \text{dbh} < 8$ cm

Trees - Woody vegetation ≥ 8 cm dbh

Litter - Dead plant material excluding downed logs

Water

Bare ground

Rocks

Downed logs - Woody vegetation ≥ 8 cm dbh and ≥ 1.5 m long

B. Tree size classes based on diameter at breast height (dbh) (modified from James and Shugart 1970).

Class Label	Dbh Range (cm)
S	$3 \leq \text{dbh} < 8$
A	$8 \leq \text{dbh} < 15$
B	$15 \leq \text{dbh} < 23$
C	$23 \leq \text{dbh} < 38$
D	$38 \leq \text{dbh} < 53$
E	$53 \leq \text{dbh} < 69$
F	$69 \leq \text{dbh} < 84$
G	$84 \leq \text{dbh} < 102$
H	$102 \leq \text{dbh}$

C. Ground cover life forms to be discriminated in circular forest plots.

Mosses

Ferns

Grasses and sedges - Narrow leafed herbaceous plants

Forbs - Broad leafed herbaceous plants

Woody ground cover - Woody vegetation ≤ 1 m tall

Seedlings - Regeneration from overstory trees, saplings, or shrubs

Litter - Dead plant material excluding slash and logs

Slash and logs - Unrooted woody vegetation (usually dead) lying prostrate

Rocks

Bare ground

Appendix II. Field data sheet for non-forest habitat (≤ 25 percent cover by trees).

Bird sp.	Quad	Plot	Transect	State	County	Latitude °	Latitude '	Latitude "	Longitude °	Longitude '	Longitude "	Elevation	Date	Observers

LINE INTERCEPT VARIABLES

TRANSECT INTERVAL	Bare ground	Rocks	Water	Litter	Downed logs	Mosses	Grasses	Forbs	Woody veg. (< 1m tall)	Shrubs(≥ 1m tall, <3cm dbh)	Saplings (3≤dbh<8)	Trees (dbh≥ 8)
1												
2												
3												
4												
5												

NEAREST TREE IN EACH QUARTER

	NE				SE				SW				NW			
POINT	Species	Dist.	DBH	Hgt.	Species	Dist.	DBH	Hgt.	Species	Dist.	DBH	Hgt.	Species	Dist.	DBH	Hgt.
1																
2																
3																
4																
5																

NEAREST SHRUB IN EACH QUARTER

	NE			SE			SW			NW		
POINT	Species	Dist.	Hgt.	Species	Dist.	Hgt.	Species	Dist.	Hgt.	Species	Dist.	Hgt.
1												
2												
3												
4												
5												

VERTICAL FOLIAGE DENSITY (# of contacts in each height interval)

	0-0.3m					0.3-1 m					1-2 m					2-9 m					> 9 m				
POINT	N	E	S	W	T	N	E	S	W	T	N	E	S	W	T	N	E	S	W	T	N	E	S	W	T
1																									
2																									
3																									
4																									
5																									

Appendix III. Field data sheet for forest habitats (> 25 percent cover by trees).

1-4 Bird sp.	5-8 Quad	9-11 Plot	12-15 Circle	16-17 State	18-20 County	Latitude ° 21-22	Latitude ' 23-24	Latitude " 25-26	Longitude ° 27-29	Longitude ' 30-31	Longitude " 32-33	34-37 Elevation	38-41 Distance to edge	42-46 Date	47-52 Observers

1-8 TREE Genus species	9-11 S 3-8 cm	12-14 A 3-15	15-17 B 15-23	18-20 C 23-38	21-23 D 38-53	24-26 E 53-69	27-29 F 69-84	30-32 G 84-102	33-35 H >102

SHRUBS Number of stems intersected

	N	S	E	W
Decid.	1-2	3-4	5-6	7-8
Conif.	9			

NEAREST TREE & LARGEST LOG IN EACH QUARTER

	Tree		Log(≥ 5m long ≥8cm diam		
	Dist.	DBH	Dist.	Diam.	Length
NE	17-20	21	22-25	26	27-29
SE	30				
SW	43				
NW	56				

DISPERSION INDEX:

Shrubs 69-70 ____________ Ground cover 71-72 ____________

CANOPY COVER ____________ 1-3 ☐% 4-6 ☐% coniferous

GROUND COVER ____________ 7-9 ☐%

DENSITY BOARD Count squares at least 50% obscured by green vegetation.

	N	E	S	W
0-.3m(HH-JJ)	10-11	12-13	14-15	16-17
.3-1m(AA-GG)	18			
1-2m (K-T)	26			
2-3m (A-J)	34			

CANOPY HEIGHT(m)

42-45 Mean	46-49 Max	50-53 Min

SLOPE(°)

54-55

Dominant shrubs(≥ 1m tall, < 3cm dbh):

1. 1-8 ____________
2. 9 ____________
3. 17 ____________
4. 25 ____________
5. 33 ____________

Dominant ground cover (ground-1m) life forms:

1. 41 ____________
2. 47 ____________
3. 53 ____________
4. 59 ____________
5. 65 ____________

HOW TO MEASURE HABITAT—A STATISTICAL PERSPECTIVE[1]

Douglas H. Johnson[2]

Abstract.--The present workshop reflects the increasing interest in the use of sophisticated statistical analysis for relating wildlife to their habitats. Multivariate methods are useful tools and their results to date have been promising, but closer attention to scientific principles and statistical requirements will prove beneficial, particularly when wildlife-habitat studies are used as the basis for prediction and management of wildlife populations.

This paper discusses several points, some well known in theory but often not fully recognized in practice, others less well known, but ideas that should guide the researcher toward an improved study design that yields more credible results. The major points are 1) The objectives of a study must be clearly thought out and precisely stated in order to design the study properly. 2) Correlation, including its analogs regression and discrimination, is not necessarily causation. 3) If habitat variables are not measured accurately, a host of analytic problems can arise. 4) The reliability and repeatability of habitat measurements are important both statistically and biologically. 5) The question of how many observations are necessary is an open one, but a few methods for addressing the question are offered.

Key words: Correlation; errors in variables; habitat studies; reliability; research design; sample size; scientific method.

INTRODUCTION

The topic I was asked to address can be viewed quite broadly. I chose to focus on some of the problems that have been encountered in my own consultations or have been identified as potentially important in published studies. The following ideas are not new, but, to judge from my experience, they are still worthy of consideration. Nor are the suggestions comprehensive, but attention to them will probably result in improved research designs.

"THE CHOICE OF A SAMPLING STRATEGY DEPENDS ON THE STUDY OBJECTIVES"

This statement is obvious, but, nonetheless, it seems too frequently disregarded, particularly in studies intended by investigators to "learn all we can." I will illustrate the point in a simplified example. Suppose we are interested in bobolinks (Dolichonyx oryzivorus) in grasslands of North Dakota. If I hold as the prime objective an accurate estimate of bobolink breeding density, I might proceed as follows. Stratify the state into regions based on physiography and/or prior

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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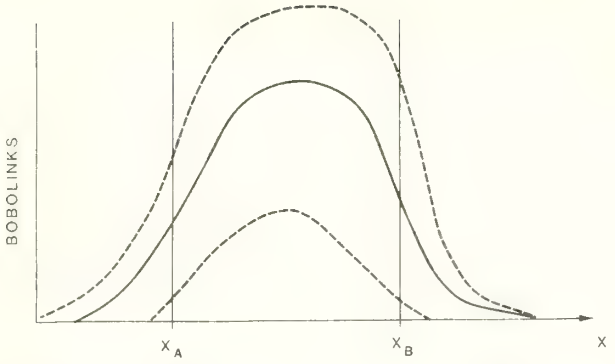

Figure 1. Hypothetical curve indicating the response of a species to an environmental gradient X. Solid line indicates average density; dashed lines denote range in density.

knowledge of bobolink densities. Select sample units of land within each stratum, the sample size proportional to the area of the stratum and to the anticipated standard deviation of bobolink counts. Suppose the bobolink responds to some habitat gradient X, which might be an east-west gradient in precipitation, as shown in figure 1. The average density is indicated by the solid line; the dashed lines denote ranges and reflect variability about the average. To estimate most accurately the mean bobolink density, I would sample most intensively those strata containing land units with values of the habitat gradient between X_A and X_B, where bobolink densities, and their standard deviations, are greatest. I would sample at a low rate the strata of marginal habitats, in which $X < X_A$ or $X > X_B$. Random sampling is necessary here to insure valid estimators of the precision of the mean. As a sideline, I might also measure vegetational features associated with each sample unit.

If, on the other hand, I am not so interested in estimating density as I am in determining relationships between bobolinks and grassland habitat features, perhaps for predictive or management purposes, I would proceed differently. I would then sample the units as much throughout the feasible region as possible, trying to get points all along the gradient. I would be particularly interested in marginal habitats for bobolinks, because some features there are presumably limiting the bird, and those features merit detailed study. Random sampling in this situation may help eliminate misleading results caused by selecting nonrepresentative units.

In general, when the objective of estimating the mean is foremost, we should sample most intensively where birds are common. If we are interested in determining relationships, we should sample more evenly along the gradient of habitat features. This is but a simple example of how specific objectives dictate the design of research and analysis of data that result.

"CORRELATION IS NOT NECESSARILY CAUSATION"

This caveat needs to be remembered as we proceed with linear or nonlinear models involving numerous and often highly intercorrelated variables, all of which are uncontrolled by the investigator. Educational statistics provide a classic example. Among grade school children, performance on scholastic achievement tests is positively correlated with body weight. Yet parents, desirous of improving their childrens' scores, would be ill-advised to fatten them in preparation for testing, because the correlation is spurious: older children tend to perform better in the tests than younger ones, and they also are likely to be heavier. This example may be so obvious as to appear trite, but the analogous situation can occur readily and less overtly in wildlife-habitat studies, in which the plethora of variables and paucity of knowledge about their true relationships can promote misconceptions. Given enough variables and access to a high-speed computer, nearly anyone can find a "significant" association among some of the variables.

"ERRORS IN VARIABLES CAN BE TROUBLESOME"

Consider the linear model

$$Y = B_0 + B_1X_1 + B_2X_2 + \dots + B_kX_k + \text{error}. \qquad (1)$$

This form ordinarily represents a regression model but discriminant analysis can be viewed in the same manner if Y is a dummy-variable indicator of group membership (Lachenbruch 1975).

In the usual formulation, the X's are assumed fixed and known quantities, measured without error. In actual practice, however, particularly in ecological work in which the X's are habitat measurements, errors of unknown magnitude often creep in. I personally suspect them to be large more often than not.

Errors in the X's lead to biases in the regression coefficients. A bias is induced whether errors are systematic, reflecting a bias, or simply random, reflecting added variability. Suppose the true relationship between, say, bird density Y and a vector of habitat features $\underline{X}$ is given by equation (1), but the X's are not measured exactly; instead $\underline{Z}$ is measured, where $\underline{Z} = \underline{X} + \underline{\delta}$ and $\underline{\delta}$ is an error of measurement. Many sources of error may contribute to $\underline{\delta}$. For example, sampling variability is usually present; the entire habitat of the animal is not measured, only a sample of it. There is often instrument error; the measured variable may not be exact. Temporal variability may contribute (Whitmore 1979); habitat measurements may not reflect conditions at the time the animals selected the habitat. More generally, the wrong variable may be measured because the correct one is not known.

Suppose that $\underline{Z}$ is unbiased for $\underline{X}$, that is $E(\underline{\delta}) = \underline{0}$, and the variance-covariance matrix of $\underline{\delta}$ is D, a diagonal matrix. The diagonality implies that errors associated with measurements of different habitat features are uncorrelated.

The regression coefficients are biased (Davies and Hutton 1975, Seber 1977), and the bias vector can be estimated by $n(Z'Z)^{-1}\hat{D}\hat{\beta}$. Z is the matrix containing the $\underline{Z}$ vectors for all observations and n is the sample size. Note that the biases tend to increase in absolute magnitude as $\hat{D}$ becomes large and as Z'Z becomes less well conditioned. That is, the biases increase when measurement errors increase and when highly correlated variables are included. These two conditions are, I believe, very common in ecological practice.

Errors in measured variables affect not only the estimated coefficients, but also their standard errors. The biases here might be either positive or negative, depending on values of the coefficients and the variances (Bloch 1978). Generally, however, the magnitude of the biases will not be unduly large if errors of measurement are reasonably small (Hodges and Moore 1972, Davies and Hutton 1975). Regardless of whether the standard error is biased positively or negatively, in the case of one explanatory variable, the "*t*" statistic for assessing the significance of that variable will be biased low (Bloch 1978). This feature could cause a truly important habitat variable to be eliminated as nonsignificant. Also, the multiple correlation coefficient may be diminished (Cochran 1970), possibly to the point that the entire set of explanatory variables is nonsignificant.

Errors in measured variables tend to deflate regression coefficients associated with those variables and to lead an ecologist to claim unjustly that their effects are insignificant. The impact of this problem may be particularly severe when the resulting models are used for prediction and/or management. Hodges and Moore (1972) noted that any bias in the regression coefficients will be transmitted into a biased forecast. They also reported several studies in which predictions were available based either on accurately measured predictor variables or on inaccurate (preliminary) values of those variables. The increased error resulting from the use of inaccurate variables was often striking.

The problem of errors in variables is often glossed over by use of a conditional argument. The relationship between Y and $\underline{X}$ is explored, *given* that values of $\underline{X}$ were observed values $\underline{Z}$. This line of reasoning is not clearly stated, perhaps not clearly understood, and certainly of minimal value in prediction and management; the manager is not interested only in habitats possessing those exact values.

The general problem of errors in variables seems to have been ignored in ecology; most applications have been in economics. Moreover, most attention has been given to multiple regression, although limited work has been done with factor analysis (Lawley and Maxwell 1973, Chan 1977).

Davies and Hutton (1975) and Seber (1977:159) presented some working rules for evaluating the effect of errors in variables. If an independent batch of data is available, it is instructive to calculate the *reliability* of each measurement:

$$\begin{aligned} g_i &= \mathrm{Var}(X_i)/\mathrm{Var}(Z_i) \\ &= \mathrm{Var}(X_i)/[\mathrm{Var}(X_i) + \mathrm{Var}(\delta_i)]. \end{aligned}$$

Reliability values appreciably below 1 should raise some suspicions about the role of the corresponding variable in the analysis.

At least until the problem is more fully explored, it seems prudent to design ecological studies so that habitat features are accurately measured and relatively independent of one another.

"VARIABLES SHOULD BE MEASURED RELIABLY"

The argument just offered suggests that habitat variables should be measured accurately, in order to reduce D as much as possible and minimize bias in the regression coefficients. There is a further reason for improved reliability: measurements should be repeatable. This feature will become increasingly valuable as studies evolve from their local orientation involving single study areas and are replicated by different researchers in different locations. To truly define the niche of a species requires studies beyond a single woodland; the species must be studied in many parts of its range. To that end, it is mandatory that measurements be reliable and without serious variability due to observer, season, occasion, or other causes.

Precious little is known about intra-observer and inter-observer sources of variability in habitat measurements, and how they compare with differences that are of interest. Ecologists either do not like to make these comparisons or, if they do, prefer not to discuss them.

THE FINAL QUESTION - "HOW LARGE A SAMPLE?"

As a consulting statistician, the first question I am usually asked is how many observations are necessary. I generally respond with one of three numbers: 1, 50, or "great gobs." The former answer, 1, is given occasionally when I believe the hypothesis is stated incorrectly, or in too much generality; a single observation is likely to refute it. The latter answer, great gobs, is given when no hypothesis is at hand, or, if there is one, it is so slippery as to evade capture and possible rejection. Neither answer satisfies the biologist, of course, but either serves as a necessary prelude to sitting down and thinking about an appropriate hypothesis. The middle answer, 50, or possibly 100 or 10 or 30, is given when the hypothesis is well stated and the experimental procedures thoughtfully described.

I can only give here some general guidelines for determining sample size. First, more observations are needed when the number of variables is large. Many published studies have only slightly more observations than variables, or sometimes even fewer. An appropriate minimum sample size might be 20 observations, plus 3 to 5 more for each variable in the analysis. Larger sample sizes help to overcome difficulties caused by violations of the assumptions of multivariate methods (Green 1979:165).

Second, examine the stability of the estimates, both means and variances. This can be done in several ways, for example, by sampling sequentially, until the mean and variance stabilize. Once the data have been gathered, the stability of the results can be assessed by subsampling, jackknifing, leaving-one-out methods, etc. If the data set is split randomly into two halves, does each half yield conclusions consistent with the other? Better yet, apply the results to another area, or a different year. What predictive value do they have?

Third, investigate the sources of variability, and how they compare in magnitude. Observer variability, temporal variability, variability in measurement method, and others all add up to cloud the variability between features that animals may be responding to. Calls for larger samples are the "knee-jerk" reaction when variability is excessive, but it may be far more advantageous to try instead to reduce this variability by better design.

CONCLUSIONS

It is useful to distinguish two kinds of research, exploratory and confirmatory. In exploratory investigations, the researcher is simply trying to "see what's going on" with respect to a system. This preliminary reconnaissance is for the purpose of hypothesis generation and will likely entail at least a cursory examination of many variables, in order to determine those that might be influential. In exploratory research, a variety of stepwise and ad hoc procedures are acceptable. Results of an exploratory investigation are hypotheses for further testing, not well founded conclusions on which management practices can credibly be based. For the more definitive answers necessary for prediction and management, confirmatory research is needed.

A confirmatory investigation is more in the mold of a classic scientific experiment, in which a hypothesis is stated, an experiment conducted to test that hypothesis, and the outcome used either to reject the hypothesis or to retain it. It is clear that this research, unlike the exploratory investigation, demands a precise hypothesis, clearly stated and unambiguous. The design also needs to be rigorous and the analysis must be statistically correct. A fresh set of data must be brought up; the data used in the exploratory stage to generate a hypothesis cannot be resurrected in the confirmatory stage to test it. Confirmatory research is more difficult to apply to ecological problems than is an exploratory investigation, but management of ecological systems requires the more definitive methods if it is to prove successful. The following suggestions are offered for an investigator planning a confirmatory study of habitat in relation to wildlife. [Green (1979) presented "ten principles" for environmental studies, many of which are equally applicable to wildlife-habitat studies.]

1. Think carefully about the objectives of the study and ask yourself, and other qualified scientists, if the procedures are truly designed to meet those objectives.

2. Remember that correlation (as well as regression and discrimination) is not necessarily causation.

3. Try to obtain habitat measurements that are relatively uncorrelated, to avoid the bias associated with the errors-in-variables problem, and for other good reasons as well. This approach appears far preferable to many ex post facto methods for reducing the number of variables, such as stepwise procedures and principal components analysis.

4. Learn about the kinds of variability in the measurements. Would the same values be obtained tomorrow as today? Would another qualified investigator record the same values? How different would another randomly selected point be? Answers to questions such as these will not only help assess the bias due to the errors-in-variables problem, they will also facilitate cooperative and comparative studies.

5. Sample sizes should be large, especially in relation to the number of variables involved. Samples should be large enough to yield stable and reliable estimates, but methods of reducing the inherent variability of measurements may be more fruitful than simply increasing the sample size.

6. And finally, for the ecologist, consult your friendly neighborhood statistician. Consult him early, in the project design phase. Consult him often, as data-gathering proceeds. Then, when you consult with him about analysis and interpretation, he will be of much better humor and of far greater benefit to you.

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DISCUSSION

JIM WOEHR: Is a distribution of plots systematically with respect to space a random sample of plants?

DOUGLAS JOHNSON: No, but it may be adequately represented by a model of randomness. The crucial issue is to define the population of which the sample is representative. Random sampling insures that condition if the sample is infinitely large, although finite ones can certainly be misrepresentative. The Bayesian concept of exhangeability is analogous.

The immediate question is whether the plants might conceivably vary sysmatically in space. In North Dakota, for example, plots located 1 mile apart might not give a representative portrayal of the plants. If the initial transect was along a roadside, most subsequent ones would be also, and smooth brome (*Bromis inermis*), for instance, would appear much more commonly in the plots than in the state as a whole. An interval of a different length between plots could yield rather accurate results, however.

Multivariate Methods

DISCRIMINANT ANALYSIS IN WILDLIFE RESEARCH: THEORY AND APPLICATIONS[1]

Byron Kenneth Williams[2]

Abstract.--Discriminant analysis, a method of analyzing grouped multivariate data, is often used in ecological investigations. It has both a predictive and an explanatory function, the former aiming at classification of individuals of unknown group membership. The goal of the latter function is to exhibit group separation by means of linear transforms, and the corresponding method is called canonical analysis. This discussion focuses on the application of canonical analysis in ecology. In order to clarify its meaning, a parametric approach is taken instead of the usual data-based formulation. For certain assumptions the data-based canonical variates are shown to result from maximum likelihood estimation, thus insuring consistency and asymptotic efficiency.

The distorting effects of covariance heterogeneity are examined, as are certain difficulties which arise in interpreting the canonical functions. A "distortion metric" is defined, by means of which distortions resulting from the canonical transformation can be assessed. Several sampling problems which arise in ecological applications are considered. It is concluded that the method may prove valuable for data exploration, but is of limited value as an inferential procedure.

Key words: Canonical analysis; covariance heterogeneity; discriminant analysis; eigenvector.

INTRODUCTION

Discriminant analysis is a technique which has come to be much used in ecological investigations. It is applicable to the study of niche breadth, niche overlap, resource partitioning, habitat selection, community structure, and many other topics. In fact the methodology is potentially useful for any ecological situation in which an association is desired between well defined groups and a set of ecologically meaningful measurements.

The data for a discriminant analysis comes to the investigator in the form of a categorical "response" variate and a corresponding set of (usually continuous) "predictor" variates. One of the objectives of the analysis is to predict the category to which an observation belongs, based on values of the predictor variates and an appropriate underlying statistical model. Such a formulation is essentially classificatory, and the prediction equations which result are called classification functions. Alternatively, the

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[1] Paper presented at The Use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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Table 1. Examples of discriminant analysis from the ecological literature. A number of measurements are made on each sample, and samples are aggregated into groups according to a grouping index.

Groups defined by	Observation measurements	Authors
Faunal species	habitat structural characteristics	Green (1971, 1974); James (1971); Bertin (1977); Cody (1978); Dueser and Shugart (1978, 1979)
Vegetation species	faunal species abundances	Ricklefs (1977)
Species presence/ absence	habitat structural characteristics	Anderson and Shugart (1974); Conner and Adkisson (1976)
Animal behavior	habitat structure, climate	Conroy et al. (1979)
Season	photosynthetic rates	Kowal et al. (1972)
Species and sex	behavioral measurements	Conley (1976)
Geographic area	vegetation densities	Norris and Barkham (1970)
Abiotic categories	habitat factors	Smith (1977)
Artificial classes	vegetation densities	Grigal and Goldstein (1971); Goldstein and Grigal (1972)
Faunal species	meristic and morphometric characteristics	Montanucci (1978)
Faunal species	song and feeding behaviors 1978c)	Rice (1978a, 1978b,
Geographic area	faunal abundance	Buzas (1967)
Soil groups	chemical concentrations	Horton et al. (1978)
Socially defined breeding demes	body measurements	Buechner and Roth (1974)

objective of the discriminant analysis may be to establish optimal "separation" of groups, based on certain linear transforms of the predictor variates. This latter approach aims at interpretation as well as prediction, and the linear functions used to explain group separation are called canonical variates. As indicated below, under certain distribution assumptions the classification approach to discriminant analysis is logically consequent to the canonical analysis. It can be shown (Williams, publication submitted) that the canonical variates themselves may be used to develop a classification procedure entirely equivalent to that produced by the predictive methodology.

Applications of discriminant analysis in the ecological literature are many and varied. A substantial proportion of these, though by no means all, concern the assessment of species-habitat associations. There is a preponderance of applications to avifauna and, to a lesser degree, to small mammals. Many are single-species studies in which groups are determined by presence or absence of an individual species. Table 1 displays some examples of the use of discriminant analysis reported in the literature. As indicated in the table, the grouping index can range over many different attributes, from vegetation types to faunal species to artificial classes built by clustering procedures. The corresponding measurement variables can range over a variety of habitat measurements, such as plant densities or vegetation structure characters, and faunal measurements such as species abundance or behavioral and morphological characteristics.

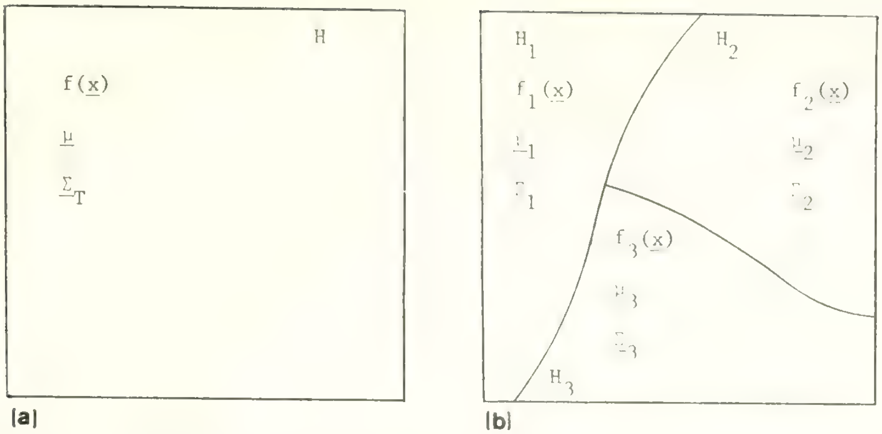

Figure 1. Partition of an environment by species utilization. (a) The unpartitioned environment, at each point of which there corresponds a vector $\underline{x}$. (b) The environment partitioned into species-specific habitats.

Most of these studies involve the use of canonical variates at some point in the investigation. Observations are plotted in a "canonical space" of reduced dimensionality, and the patterns displayed are interpreted. Attempts generally are made to interpret the canonical functions themselves, often by an examination of coefficients. These efforts are hampered by certain statistical and conceptual difficulties which arise in applications with ecological data.

In view of the increasing use of canonical variates in ecological investigations, this paper focuses on the theory and applications of canonical analysis. For purposes of elucidation the general probability model for discriminant analysis is introduced below, along with a brief description of linear classification based on it. Then canonical analysis is investigated from the point of view of vector transformations. My goal is to specify precisely the model, the estimation procedures and the geometric logic of canonical analysis. A geometric approach, by clarifying the structure of canonical analysis, reveals the importance of its statistical assumptions and the possible consequence of their violation.

PROBABILITY STRUCTURE

The probability structure to which discriminant analysis applies is specified as follows. Consider a mixture of g populations $\pi_1,\ldots,\pi_g$ with mixing proportions $q_1,\ldots q_g$, represented by the vector $\underline{q}$. Associated with each individual in the mixture is a vector $[i,\underline{x}']'$ of p+1 components, the first of which (i) specifies population membership. The remaining p components in $\underline{x}$ are a set of measurement values associated with the individual. Random selection from the mixture defines a random variable I for population membership and a random vector $\underline{X}$ of measurement values. The probability structure of the mixture is defined by a set of distributions:

(i) $P\ (I = i) = q_i$

the probability that an individual chosen at random from the mixture is in population π_i (the values in $\underline{q}$ are often called prior probabilities);

(ii) $f_{X|I}(\underline{x}|i) = f_i(\underline{x})$,

the conditional distribution of $\underline{X}$ over the population π_i. If the set of conditional distributions $f_1(\underline{x}),\ldots,f_g(\underline{x})$ is given as the vector $\underline{f}$, then the mixture is represented by an ordered pair $(\underline{f},\underline{q})$.

For the ensuing discussion it may be of value to think of the sampling universe, denoted by H, as a habitat which is partitioned by way of species utilization. A set of habitat variables is measured on each sample plot, for example canopy height, ground cover and shrub density. These variables have a frequency distribution $f(\underline{x})$ over the habitat H with mean $\underline{\mu}$ and covariance $\underline{\Sigma}_T$.

In addition, each plot has associated with it a variable which indicates which species utilizes it. This variable partitions H into specific habitats, each with its own frequency distribution $f_i(\underline{x})$ of habitat variables. The proportion of H which is included in the habitat of species i is q_i. Such a partitioning is shown in figure 1 for three groups.

Figure 1(a) indicates the sampling universe H, over which can be measured vector values of $\underline{x}$. The distribution of $\underline{x}$ over H is given by $f(\underline{x})$, with mean $\underline{\mu}$ and covariance $\underline{\Sigma}_T$. No partitioning principle is involved in this distribution. In Figure 1(b) H has been partitioned into three subsets. The values that $\underline{x}$ can take in subset H_i define the conditional distribution $f_i(\underline{x})$ with mean $\underline{\mu}_i$ and covariance $\underline{\Sigma}_i$. Mixing proportions q_i specify the proportion of H constituted of H_i, and the relationship of moments in partitioned and unpartitioned spaces is given by

$$\underline{\mu} = q_1\underline{\mu}_1 + \dots + q_g\underline{\mu}_g$$

and

$$\underline{\Sigma}_T = \bar{\underline{\Sigma}} + \underline{A},$$

where

$$\bar{\underline{\Sigma}} = q_1\underline{\Sigma}_1 + \dots + q_g\underline{\Sigma}_g$$

and

$$\underline{A} = \sum_{i=1}^{g} q_i(\underline{\mu}_i - \underline{\mu})(\underline{\mu}_i - \underline{\mu})'.$$

It is, of course, not required of the specific habitats that their corresponding measurements $\underline{x}$ be grouped into disjoint sets. H_i and H_j may both contain plots characterized by the same measurements $\underline{x}$, and in fact the range of measurements may be identical over H_i and H_j. It is necessary, however, that the statistical distribution of habitat values differs across species. Discriminant analysis seeks to highlight these among-group statistical differences.

CLASSIFICATION PROCEDURES

The classification problem may be stated in terms of the structure exhibited above: to predict population membership for an individual chosen from $(\underline{f},\underline{q})$, given that $\underline{X} = \underline{x}$. Stated differently, the problem is to classify individuals into one of the g populations based on observed values $\underline{x}$. Classification is determined by

$$P[I = i \mid \underline{X} = \underline{x}],$$

the probability that a sampling unit with observed values $\underline{x}$ is a member of population π_i. A procedure which minimizes classification error is to assign an individual to π_i if

$$P[I = i \mid \underline{X} = \underline{x}] = \max\ \{P[I = j \mid \underline{X} = \underline{x}] : j = 1,\dots,g\}.$$

Since

$$P[I=i \mid \underline{X} = \underline{x}] = \frac{q_i f_i(\underline{x})}{\sum_{j=1}^{g} q_j f_j(\underline{x})}$$

this procedure is equivalent to classification based on

$$q_i f_i(\underline{x}) = \max\ \{q_j f_j(\underline{x}) : j=1,\dots,g\}.$$

The earliest and best developed discriminant methodology assumes a multivariate normal distribution. That is, the conditional distribution of predictor variates is given by

$$f_i(\underline{x}) = (2\pi)^{-p/2}\ |\underline{\Sigma}_i|^{-1/2}\ \exp[-1/2(\underline{x}-\underline{\mu}_i)'\underline{\Sigma}_i^{-1}(\underline{x}-\underline{\mu}_i)],$$

where i indexes population π_i and $\underline{\mu}_i$, $\underline{\Sigma}_i$ are the corresponding mean vector and covariance matrix. Linear discrimination results for the assumption of covariance homogeneity:

$$\underline{\Sigma}_i = \underline{\Sigma},\ i=1,\dots,q.$$

In this case the conditional distributions can be rewritten in group-specific terms:

$$\begin{aligned} f_i(\underline{x}) &= (2\pi)^{-p/2}|\underline{\Sigma}|^{-1/2}\exp[1/2\underline{x}'\underline{\Sigma}^{-1}\underline{x}] \cdot \\ &\qquad \exp[(\underline{x} - 1/2\ \underline{\mu}_i)'\underline{\Sigma}^{-1}\underline{\mu}_i] \\ &= w(\underline{x})\exp[(\underline{x} - 1/2\ \underline{\mu}_i)'\underline{\Sigma}^{-1}\underline{\mu}_i], \end{aligned}$$

where $w(\underline{x})$ is free of group-specific parameters $\underline{\mu}_i$.

For these distributions the optimal classification rule may be simplified by noting that

$$q_i f_i(\underline{x}) \geq q_j f_j(\underline{x})$$

if and only if

$$\ln q_i + \ln f_i(\underline{x}) \geq \ln q_j + \ln f_j(\underline{x}).$$

Since

$$\ln f_i(\underline{x}) = \ln w(\underline{x}) + (\underline{x} - 1/2\ \underline{\mu}_i)'\underline{\Sigma}^{-1}\underline{\mu}$$

and $\ln\ w(\underline{x})$ has no discriminating power, the classification rule can be specified with the linear function

$$L_i(\underline{x}) = (\underline{x} - 1/2\ \underline{\mu}_i)'\underline{\Sigma}^{-1}\underline{\mu}_i + \ln q_i.$$

The procedure is to classify an observation into group i, based on the observed values $\underline{x}$, if

$$L_i(\underline{x}) = \max\ \{L_j(\underline{x}) \mid j=1,\dots,g\}.$$

This is simply Fisher's linear discriminant function (Fisher 1936). When $\underline{\mu}_i$, $\underline{\Sigma}$, and q_i are unknown, the maximum likelihood estimates may be used in the expression for $L_i(\underline{x})$. A substantial body of literature exists on the statistical consequences, especially in error rate analysis, of this replacement (see, e.g., Toussaint 1974).

SAMPLE-BASED CANONICAL ANALYSIS

A different approach to discrimination, which sometimes yields additional information about group differences, is based on the use of canonical transformations. The usual data-based methods of canonical analysis involve the determination of linear transforms

$$z = \underline{a}'\underline{x}$$

which maximize

$$\sum_{i=1}^{g} n_i(\bar{z}_i - \bar{z})^2 / \sum_{i=1}^{g} \sum_{j=1}^{n_i}(z_{ij} - \bar{z}_i)^2,$$

where

$$\bar{z}_i = \underline{a}'\underline{\bar{x}}_i$$

and

$$\bar{z} = \underline{a}'(1/n \sum_{i=1}^{g} n_i\underline{\bar{x}}_i).$$

In these expressions n_i is the sample size for population π_i and $n = \sum_{i=1}^{g} n_i$. If the data for a sample from the mixture $(\underline{f},\underline{q})$ are aggregated by

$$\underline{T} = \sum_{i=1}^{g} \sum_{j=1}^{n_i}(\underline{x}_{ij} - \underline{\bar{x}})(\underline{x}_{ij} - \underline{\bar{x}})'$$

$$= \sum_{i=1}^{g} \sum_{j=1}^{n_i}(\underline{x}_{ij} - \underline{\bar{x}}_i)(\underline{x}_{ij} - \underline{\bar{x}}_i)'$$

$$+ \sum_{i=1}^{g} n_i(\underline{\bar{x}}_i - \underline{\bar{x}})(\underline{\bar{x}}_i - \underline{\bar{x}})'$$

$$= \underline{W} + \underline{B},$$

then the procedure above is formally equivalent to finding eigenvectors corresponding to the g-1 non-zero eigenvalues from

$$[\underline{B} - \lambda\ \underline{W}]\ \underline{a} = \underline{0}.$$

These eigenvectors define g-1 canonical variates

$$z_i = \underline{a}_i'\underline{x},\ i=1,\ldots,g-1$$

which are often described as linear transforms which "maximize among-group variation relative to within-group variation."

PARAMETRIC CANONICAL ANALYSIS

Under certain probability conditions this intuitive and essentially non-parametric method can be generated by a parametric procedure which considers linear transformations of population means. The goal once again is to establish separation of group means, but in this instance the focus initially is on population differences and the parameters characterizing them. Data enters the analysis by way of parameter estimation, at which point the appropriate computing forms can be developed. This approach in some sense reverses the foregoing data based analysis: rather than manipulating data into a statistic by which to interpret sample structure, a geometric focus emphasizes the parametric structure which then is estimated with the data. The intended result from this orientation is a sharpening of the assumptions for canonical analysis and a clarification of its utility for inferences in ecological studies.

Consider the group means $\underline{\mu}_i$, $i=1,\ldots,g$ and common dispersion $\underline{\Sigma}$. We seek in the canonical analysis to describe the separation of these means in a statistically meaningful way. The global mean of the population mixture $(\underline{f},\ \underline{q})$ is given by

$$\underline{\mu} = \sum_{i=1}^{g} q_i\underline{\mu}_i,$$

and the population deviations $\underline{\mu}_i - \underline{\mu}$ are defined by the difference between group and overall means. Let L be any arbitrary line through $\underline{\mu}$ with direction cosines $\underline{a}$. Then the projection of $\underline{\mu}_i - \underline{\mu}$ onto L is a vector with squared length given by

$$d_i^2 = [\underline{a}'\ (\underline{\mu}_i - \underline{\mu})]^2$$

$$= \underline{a}'(\underline{\mu}_i - \underline{\mu})(\underline{\mu}_i - \underline{\mu})'\underline{a}.$$

The average of squared lengths is

$$\sum_{i=1}^{g} q_i d_i^2 = \sum_{i=1}^{g} q_i\underline{a}'(\underline{\mu} - \underline{\mu})(\underline{\mu} - \underline{\mu})'\underline{a}$$

$$= \underline{a}'\ [\sum_{i=1}^{g} q_i(\underline{\mu}_i - \underline{\mu})(\underline{\mu} - \underline{\mu})']\underline{a}$$

$$= \underline{a}'\underline{A}\ \underline{a},$$

which is maximum for some particular direction $\underline{a}^*$ of the projection line. It can be shown that $\underline{a}^*$ is the dominant eigenvector of $\underline{A}$. The optimal direction which is orthogonal to $\underline{a}^*$ is given by the second dominant eigenvector of $\underline{A}$, and so on. Since $\underline{A}$ is of rank g-1 there exist g-1 orthogonal directions by which to separate means, corresponding to the non-zero eigenvalues of $\underline{A}$.

The use of $\underline{a}^*$ (and the remaining eigenvectors) to separate group means is optimal in the sense that for no other projection line is the average of squared distances between means as large. This method is suboptimal, however, in that it does not account for variances and covariances within each population. The failure to accomodate the covariance structure can lead to two highly undesirable results. First, variates with high variation (and therefore low information content) have the same influence on the analysis as do variates with low variation (and high information content). Second, the effect of weighting highly correlated variables equally is to base the analysis less on statistical content than merely on the number of variates included in it. In such a situation one could force group separations to reflect any arbitrarily chosen variate merely by including additional positively correlated variates in the analysis. Such distortions and abritrariness are precisely the kinds of effects which motivate the use of $\underline{\Sigma}^{-1}$ in the Mahalanobis distance formula.

Canonical analysis includes the same adjustment, the effect of which is to eliminate covariances and unequal variances. This adjustment utilizes a square-root factorization $\underline{\Sigma}^{1/2}$ of $\underline{\Sigma}$ to define new variables

$$\underline{x}^* = \underline{\Sigma}^{-1/2}\underline{x}$$

with conditional mean $\underline{\Sigma}^{-1/2}\underline{\mu}_i$ and identity covariance (Graybill 1976). Thus the original variates are transformed into unit variance, uncorrelated variates, eliminating ambiguities and distortions.

The same projection argument as above may be used on the transformed means $\underline{\Sigma}^{-1/2}\underline{\mu}_i$. The corresponding deviations are

$$\underline{\Sigma}^{-1/2}(\underline{\mu}_i - \underline{\mu}),$$

and the least squares lines fitting these deviations are based on a spectral decomposition of

$$\sum_{i=1}^{g} q_i\, \underline{\Sigma}^{-1/2}(\underline{\mu}_i - \underline{\mu})(\underline{\mu}_i - \underline{\mu})'\, \underline{\Sigma}^{-1/2}$$

$$= \underline{\Sigma}^{-1/2}\, \underline{A}\, \underline{\Sigma}^{-1/2'}.$$

The corresponding matrix equation is

$$[\underline{\Sigma}^{-1/2}\, \underline{A}\, \underline{\Sigma}^{-1/2'} - \lambda\, \underline{I}]\, \underline{v} = \underline{0},$$

which may be written as

$$\underline{\Sigma}^{-1/2}\, [\underline{A} - \lambda\, \underline{\Sigma}]\, \underline{\Sigma}^{-1/2'}\, \underline{v} = \underline{0}$$

or

$$[\underline{A} - \lambda\, \underline{\Sigma}]\, \underline{u} = \underline{0}, \qquad (1)$$

where

$$\underline{u} = \underline{\Sigma}^{-1/2'}\underline{v}.$$

Canonical variates are then given by

$$\underline{z} = \underline{v}'\underline{x}^*$$

$$= \underline{v}'\, \underline{\Sigma}^{-1/2}\, \underline{x}$$

$$= \underline{u}'\, \underline{x}.$$

There are g-1 such variates, corresponding to the non-zero eigenvalues of equation (1). They may be represented by the canonical transform

$$\underline{z} = \underline{U}'\underline{x}, \qquad (2)$$

where the columns of $\underline{U}$ are vector solutions of equation (1).

In most situations none of the parameters for the population mixture is known with certainty, and they must be estimated from the data. Assume that a random sample of size n from the population mixture is obtained, n_i of which are from population π_i. Based on the multivariate normal assumption the following maximum likelihood estimates result:

$$\hat{q}_i : n_i/n$$

$$\hat{\underline{\mu}}_i : \bar{\underline{x}}_i = 1/n_i \sum_{j=1}^{n_i} \underline{x}_{ij}$$

$$\hat{\underline{\Sigma}} : \underline{S} = 1/(n-g) \sum_{i=1}^{g} \sum_{j=1}^{n_i} (\underline{x}_{ij} - \bar{\underline{x}}_i)(\underline{x}_{ij} - \bar{\underline{x}}_i)'$$

$$\hat{\underline{\mu}} : \sum_{i=1}^{g} \hat{q}_i\, \hat{\underline{\mu}}_i = 1/n \sum_{i=1}^{g} \sum_{j=1}^{n_i} \underline{x}_{ij}$$

$$\hat{\underline{A}} : 1/n\, \underline{B} = 1/n \sum_{i=1}^{g} n_i\, (\bar{\underline{x}}_i - \bar{\underline{x}})(\bar{\underline{x}}_i - \bar{\underline{x}})' \quad .$$

When these maximum likelihood estimates are used in equation (1) in place of the population parameters, the equation becomes

$$[\hat{\underline{A}} - \lambda\, \hat{\underline{\Sigma}}]\, \underline{u} = \underline{0} \qquad (3)$$

or

$$[1/n\, \underline{B} - \lambda\, \underline{S}]\, \underline{u}$$

$$= 1/n\, [\underline{B} - n/(n-g)\, \lambda\, \underline{W}]\, \underline{u}$$

$$= \underline{0}\ .$$

Equation (3) has the same eigenstructure as does

$$[\underline{B} - \lambda\, \underline{W}]\, \underline{u} = \underline{0}.$$

The effect of n/(n-g) is to scale the eigenvalues, leaving eigenvectors unchanged. This can be seen by

$$[\underline{B} - \lambda\, n/(n-g)\, \underline{W}\ ]\, \underline{u}$$

$$= \underline{W}^{1/2}\, [\underline{W}^{-1/2}\, \underline{B}\, \underline{W}^{-1/2'} - \lambda\, n/(n-g)\, \underline{I}]\, \underline{W}^{1/2'}\underline{u},$$

from which it follows that $n/(n-g)\ \lambda$ is an eigenvalue and $\underline{W}^{1/2'}\underline{u}$ the corresponding eigenvector of $\underline{W}^{-1/2}\ \underline{B}\ \underline{W}^{-1/2'}$. Therefore eigenvectors of

$$[\hat{\underline{A}} - \lambda\, \hat{\underline{\Sigma}}]\, \underline{u} = \underline{0}$$

and

$$[\underline{B} - \lambda\, \underline{W}]\, \underline{u} = \underline{0}$$

are identical. This demonstrates the equivalence of parametric and data-based approaches to canonical analysis, given the following three assumptions:

(i) the data consist of a random sample from a population mixture of multivariate normal populations;
(ii) covariances are homogeneous across all populations;
(iii) maximum likelihood estimates are used in place of parametric values.

In ecological investigations it is hoped that an intelligent sampling plan can be combined with the central limit theorem to approximately satisfy condition (i). Also, the many advantages of maximum likelihood estimation make condition (iii) a reasonable procedure. Therefore the applicability of canonical analysis in ecological investigations seems to hinge on condition (ii), the homogeneity of covariance.

It is noted parenthetically that the canonical variates in equation (2) are uncorrelated and have a variance of unity. Furthermore, it can be shown that

$$\underline{u}_i' \, \underline{A} \, \underline{u}_i = \lambda_i, \ i=1,\ldots,g-1$$

(Williams, publication submitted). Two extremely useful invariance properties follow (let the transformed population means be represented by $\underline{\eta}_i = \underline{U}'\underline{\mu}_i$, i=1...,g):

First, relative distances are maintained in canonical space. That is, if Mahalanobis distances in observation and canonical space are defined by

$$D_i(\underline{x}) = (\underline{x} - \underline{\mu}_i)' \, \underline{\Sigma}^{-1}(\underline{x} - \underline{\mu}_i)$$

and

$$D_i(\underline{z}) = (\underline{z} - \underline{\eta}_i)'(\underline{z} - \underline{\eta}_i)$$

respectively, then

$$D_i(\underline{x}) - D_j(\underline{x}) = D_i(\underline{z}) - D_j(\underline{z})$$

(Williams, publication submitted). Second, group mean differences are also maintained:

$$(\underline{\mu}_i - \underline{\mu}_j)' \, \underline{\Sigma}^{-1} \, (\underline{\mu}_i - \underline{\mu}_j)$$
$$= \ (\eta_i - \eta_j)'(\eta_i - \eta_j).$$

This last result is of obvious importance in the study of resource partitioning and niche overlap (MacArthur and Levins 1967, Harner and Whitmore 1977).

INEQUALITY OF COVARIANCES

It remains to rationalize the procedures of canonical analysis under the assumption of unequal conditional covariance matrices. Given conditions (i) - (iii) above, the canonical analysis represents a statistically meaningful attempt to optimally separate population means. Its meaning when condition (ii) is violated becomes more problematic, and obviously depends on what matrix $\underline{\Sigma}$ is used in equation (1). It should be noted that the square root transform, invoked to eliminate covariances, will most certainly fail to have its intended effect when group-specific covariances are unequal. Indeed, no matter what "covariance" matrix $\underline{\Sigma}$ is used in the analysis, the resulting conditional covariances are still heterogeneous and have the form

$$\underline{\Sigma}^{-1/2} \underline{\Sigma}_i \, \underline{\Sigma}^{-1/2'} \ .$$

In effect nothing of value for covariance stabilization has been gained by the transform, and the meaningfulness of the canonical procedure is thrown into question.

An often used approach is simply to use the overall mixture covariance $\underline{\Sigma}_T$, or to use an "average" covariance defined by

$$\underline{\Sigma} = q_1 \, \underline{\Sigma}_1 + \ldots + q_g \, \underline{\Sigma}_g. \qquad (4)$$

That these two matrices yield the same eigenstructure can be easily shown:

Since

$$\underline{\Sigma}_T = \overline{\underline{\Sigma}} + \underline{A}$$

we have

$$[\underline{A} - \lambda \, \underline{\Sigma}_T] \, \underline{u}$$
$$= [\underline{A} - \lambda \, (\overline{\underline{\Sigma}} + \underline{A})] \, \underline{u}$$
$$= [(1 - \lambda) \, \underline{A} - \lambda \, \overline{\underline{\Sigma}}] \, \underline{u}$$
$$= (1 - \lambda) \, [\underline{A} - \lambda/(1 - \lambda) \, \overline{\underline{\Sigma}}] \, \underline{u}$$
$$= \underline{0}.$$

Therefore $\underline{\Sigma}_T$ and $\overline{\underline{\Sigma}}$ yield the same eigenvectors when used in equation (1). Note that when conditional covariances are identical, $\underline{\Sigma}$ in equation (4) is simply their common value, and the equation

$$[\underline{A} - \lambda \, \underline{\Sigma}_T] \, \underline{u} = \underline{0}$$

is equivalent in its eigenvectors to equation (1). When covariances are unequal, however, both $\overline{\underline{\Sigma}}$ and $\underline{\Sigma}_T$ are defined only over the population mixture, and neither generates an eigenstructure equivalent to that based on individual dispersions $\underline{\Sigma}_i$.

One result of heterogeneous covariances is that the canonical variates are uncorrelated over the mixture ($\underline{f}$, $\underline{q}$), but not over the conditional distributions. For any given conditional population they may be highly correlated, and this greatly complicates their interpretation. Furthermore, the representation of conditional

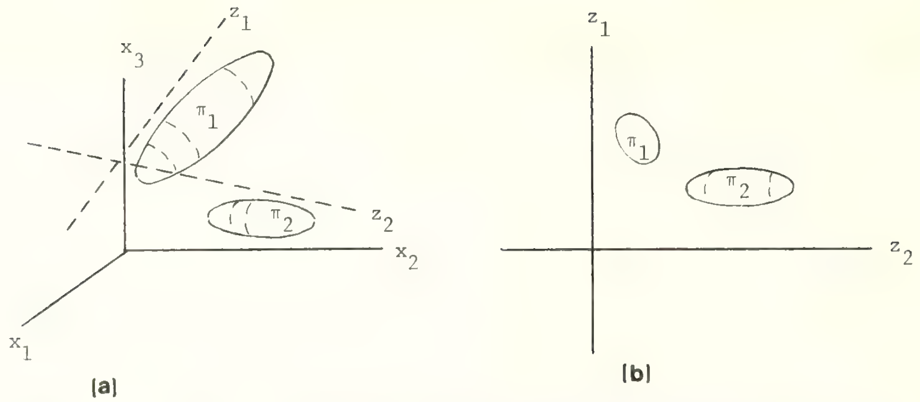

Figure 2. Population representatives in observation and canonical space. (a) The dispersion of two populations in observation space. Canonical axis are superimposed by dotted lines. (b) The sample population dispersions in canonical space.

populations in the g-1 dimensional space defined by a canonical analysis may severely distort their geometric configurations. An example is shown in figure 2.

Figure 2(a) shows two conditional distributions in observation space, one (π_1) with its dominant axis nearly orthongonal to the canonical axes z_1 and z_2. Representation of these populations in canonical space is shown in figure 2(b). Such group specific distortions result from the projection of p-variate distributions into g-1 dimensions, and they greatly complicate the interpretation of areas in canonical space. It follows that one must exercise caution in analyzing conditional population dispersions with canonical variates. This is not unexpected, since the fundamental purpose of discrimination is the assessment of group differences, rather than the analysis of dispersion.

INTERPRETATION OF CANONICAL VARIATES

The canonical analysis assumes its most obvious value for ecologists by providing interpretable transforms of data. As mentioned above, these transforms are specifically chosen to separate group means in an optimal manner. The canonical variates which result are uncorrelated linear combinations of observation variables, the coefficients in which may be given ecological interpretations. At this point in the analysis biological insight is of fundamental importance. It is, however, important to recognize certain limitations on interpretability with these transforms.

Both magnitude and sign of the canonical coefficients often are used for interpretation. Under certain conditions, e.g., when one coefficient dominates all others in the canonical transform and the correlation structure is simple, this is an acceptable practice. In such a situation it is fairly straightforward to assess the "meaning" of the canonical variate, i.e., to specify what it represents biologically. When the correlation structure is complex and there are several coefficients of significant size, however, interpretation is not so direct. The difficulty arises from the fact that the observation variables in the canonical transforms are correlated, some of them perhaps highly correlated. Individual canonical coefficients in this case reflect not only the influence of their corresponding observation variables, but also the influence of other variables as reflected through the correlation structure of the data. Most people who have worked with discriminant analysis have probably seen cases in which positively correlated variates have canonical coefficients with different signs. These apparently inconsistent coefficients indicate that the two corresponding variables include information from the remaining observation variates which influences the canonical variate in opposing ways. It can be shown (Williams, in prep.) that the correlation of the canonical variate z_i and an observation variate x_j is

$$\text{corr}\,(z_i, x_j) = 1/\sqrt{\lambda_i}\,(a^*_{ij} + \sum_{k\neq j} a^*_{ik}\,\rho_{kj}), \quad (5)$$

where a^*_{ij} is the "standardized" canonical coefficient of x_j in the i^{th} canonical transform.

This expression reveals that the effect of an observation variable on the canonical variate is only partially given by the numerical value of its corresponding coefficient. Terms involving the remaining coefficients and the correlation structure between variables also influence the association between z_i and x_j, and sometimes this latter influence is predominant. It follows that one cannot safely interpret the coefficients singly. A similar argument can be made against interpreting pairs, triples, or any subset of coefficients in a canoncal function. As one might expect, this same problem also arises in ordinary least squares regression: the values of individual parameters reflect the correlation structure of the data. For complex structures, magnitudes and even signs of coefficients are dependent on what additional variables are included in the model (Weiner and Dunn 1966). It makes little sense in that case to base one's interpretations on individual coefficients. A safer technique is to examine the correlation of the canonical variate either with individual observation variables included in the canonical analysis (5), or with ancillary information not included in it (Green 1971, James 1971, Dueser and Shugart 1978). High correlations may then provide an interpretable "meaning" of the canonical variate.

There is in the literature one other method of interpretation, about which some words of caution should be voiced. This involves the use in canonical space of "equal frequency ellipses", defined in multivariate populations by hyperellipses of constant probability density (Harner and Whitmore 1977). For a given distribution with moments ($\underline{\mu}_i$, $\underline{\Sigma}_i$), a point in observation space will be on only one such ellipse. When g populations are defined in a discrimination analysis, the observation lies on ellipses which are specific to each population. It is noted that when populations are normally distributed these ellipses are defined by Mahalanobis distances. They may be used to generate a classification methodology identical with the usual classification procedure as outlined above.

Several results concerning equal frequency ellipses follow from the equal covariance assumption. First, they intersect along straight lines in the observation space. Second, the optimal classification procedure based on them is linear. These two properties are of course equivalent, since the linear classification functions correspond to a linear partitioning of the observation space. Third, the relative distances of points in canonical space as measured by $D_i(\underline{z})$, are identical to those in observation space (Williams, publication submitted). This effectively means that equal frequency ellipses in canonical space can be used to assess the position of an observation relative to the group means: there is, in essence, no important "loss of information" about conditional distributions when canonical variates are used. Thus ecologists are justified in using the canonical variates rather than the original data to investigate ecological distributions. The invariance property is indicated below with Mahalanobis distances, using three group means and an observation vector $\underline{x}$:

Ranking	Observation Space	Canonical Space
1	$(\underline{x}-\underline{\mu}_1)'\underline{\Sigma}^{-1}(\underline{x}-\underline{\mu}_1)$	$(\underline{z}-\underline{\eta}_1)'\underline{V}^{-1}(\underline{z}-\underline{\eta}_1)$
2	$(\underline{x}-\underline{\mu}_2)'\underline{\Sigma}^{-1}(\underline{x}-\underline{\mu}_2)$	$(\underline{z}-\underline{\eta}_2)'\underline{V}^{-1}(\underline{z}-\underline{\eta}_2)$
3	$(\underline{x}-\underline{\mu}_3)'\underline{\Sigma}^{-1}(\underline{x}-\underline{\mu}_3)$	$(\underline{z}-\underline{\eta}_3)'\underline{V}^{-1}(\underline{z}-\underline{\eta}_3)$.

Since the canonical variates are uncorrelated with unit variance, the covariance $\underline{V}$ is in fact the identity matrix $\underline{I}$. The terms $(\underline{x}-\underline{\mu}_i)\underline{\Sigma}^{-1}(\underline{x}-\underline{\mu}_i)$ define equal frequency ellipses on which classification may be based, and the corresponding ellipses in canonical space are given by $(\underline{z}-\underline{\eta}_i)'\underline{V}^{-1}(\underline{z}-\underline{\eta}_i)$. Equal covariances assure identical rankings of observations in both observation and canonical space.

Unfortunately none of these characteristics obtains when covariances are unequal. In particular, the identity of rankings in canonical and observation space no longer holds. This lack of invariance may be indicated by

Ranking	Observation Space	Canonical Space
1	$(\underline{x}-\underline{\mu}_1)'\underline{\Sigma}_1^{-}d^{1}(\underline{x}-\underline{\mu}_i)$	$(\underline{z}-\underline{\eta}_i)'\underline{V}_i^{-1}(\underline{z}-\underline{\eta}_i)$
2	$(\underline{x}-\underline{\mu}_2)'\underline{\Sigma}_2^{-1}(\underline{x}-\underline{\mu}_2)$	$(\underline{z}-\underline{\eta}_j)'\underline{V}_j^{-1}(\underline{z}-\underline{\eta}_j)$
3	$(\underline{x}-\underline{\mu}_3)'\underline{\Sigma}_3^{-1}(\underline{x}-\underline{\mu}_3)$	$(\underline{z}-\underline{\eta}_k)'\underline{V}_k^{-1}(\underline{z}-\underline{\eta}_k)$.

Unequal covariances in observation space are indicated by $\underline{\Sigma}_i$, i=1,2,3. Covariances of the canonical variates are also unequal, since the canonical transform generates variates which are globally uncorrelated but conditionally correlated. $\underline{V}_i$ expresses these conditional correlations. Note that the rankings of Mahalanobis distances in canonical space are not given a priori by their rankings in observation space. Since the canonical transform

$$\underline{z} = \underline{Ux}$$

maintains rankings when covariances are equal, this shift in rankings is a direct result of covariance heterogeneity. This is shown by noting that conditional covariances for transformed and untransformed variates are related by

$$\underline{V}_i = \underline{U}\ \underline{\Sigma}_i\ \underline{U}',$$

where $\underline{U}$ is the (g-1) x p transform matrix generated in equation (1). Then Mahalanobis distances are given by

$$\begin{aligned} D_i(\underline{z}) &= (\underline{z} - \underline{\eta}_i)'\ \underline{V}_i^{-1}\ (\underline{z} - \underline{\eta}_i) \\ &= [\underline{U}\ (\underline{x} - \underline{\mu}_i)]'\ (\underline{U}\ \underline{\Sigma}_i\ \underline{U})^{-1}\ [\underline{U}\ (\underline{x} - \underline{\mu}_i)]. \qquad (6) \end{aligned}$$

The influence of $\underline{U}$ on $D_i(\underline{z}) - D_j(\underline{z})$ clearly depends on the difference between $\underline{U}\ \underline{\Sigma}_i\ \underline{U}'$ and $\underline{U}\ \underline{\Sigma}_j\ \underline{U}'$, which in turn depends on the structures of $\underline{\Sigma}_i$ and $\underline{\Sigma}_j$. Therefore the relative magnitudes of Mahalanobis distances in canonical space are a priori indeterminate.

A measure of the distortion induced by covariance heterogeneity may be defined by means of the function

$$h_{ij}(\underline{x}) = 1 \text{ if } D_i(\underline{x})=D_j(\underline{x}) \text{ or } D_i(\underline{z})=D_j(\underline{z})$$

$$= |(D_i(\underline{x})-D_j(\underline{x}))/(D_i(\underline{z})-D_j(\underline{z}))|$$

otherwise,

where $D_i(\underline{z})$ is given by equation (6) and

$$D_i(\underline{x}) = (\underline{x} - \mu_i)' \ \underline{\Sigma}^{-1} \ (\underline{x} - \mu_i).$$

This function assumes only positive values, and when covariances are equal its value is unity for all $\underline{x} \in H$. Also, as covariances become more heterogeneous the dispersion of its values increases correspondingly. Now let $h^*(\underline{x})$ be the maximum value of $1/2(h_{ij}(\underline{x}) + 1/h_{ij}(\underline{x}))$ over all i and j:

$$h^*(\underline{x}) =$$

$$\max[1/2(h_{ij}(\underline{x})+1/h_{ij}(\underline{x})):i=1,\ldots,g,$$

$$j=1\ldots g,\ i \neq j].$$

Then the canonical analysis is defined to be distortion-free (within an ε-tolerance) if

$$1 - \varepsilon \leq h^*(\underline{x}) \leq 1 + \varepsilon$$

over some appropriate proportion of the sampling universe H. Note that this condition will be met as long as relative Mahalanobis distances are approximately maintained in canonical space. Since relative distances are exactly maintained when covariances are equal, $h^*(\underline{x}) = 1$ for all $\underline{x} \in H$ and the transform is completely free from distortion.

It should be emphasized that a canonical analysis is distortion-free only for certain combinations of covariance matrices $\underline{\Sigma}_i$, $i=1\ldots,g$, and that the property cannot be automatically assumed. When the canonical procedure is not distortion-free, statistical relationships between distances in observation space and their canonical representations are complex and non-intuitive. Under such conditions one cannot base inferences about observation data on statistical characterizations in canonical space. Before the canonical analysis can be interpreted with equal frequency ellipses, distortion induced by covariance heterogeneity must be assessed.

A practical consequence for ecologists is that, contrary to the case with equal covariances, one cannot safely use equal frequency ellipses in canonical space for interpreting group differences. The inferences drawn from the canonical analysis are not translatable back to the observation space, because distance measures (and the corresponding probability measures) are distortted by the canonical transform. One conclusion seems inescapable: the canonical analysis, which possesses so many positive geometric and statistical properties for homogeneous covariances, is fraught with problems and ambiguities otherwise. Any recommendation to use this methodology when covariances are demonstrably unequal should be cautiously offered, and cautiously accepted. While heterogeneity of covariance may in fact result in no major misinterpretations, this is by no means a certainty. The point of this discussion is that the canonical analysis requires specific well-defined assumptions, violations of which may have unforeseen and potentially serious distorting effects. The canonical analysis then becomes an ad hoc procedure for generating linear data transforms which may or may not focus the researcher's attention on meaningful relationships. The hope that it will suggests that there may be value in the methodology, even when its assumptions fail. The same claim of course can be made of any data analysis procedure, or indeed of any activity whatever.

CONCLUSIONS

This discussion has focused on a parametric development of canonical analysis and its relationship to the usual data-based approach suggested by Fisher (1936). Notwithstanding the problems associated with covariance heterogeneity, it is fortuitous that maximum likelihood estimation for normal populations yields the familiar computing forms. This insures consistent, asymptotically efficient estimators. Nevertheless, there remain a number of problems concerning the effects of sampling. For example, nothing has been said about small sample variability, rates of convergence, and possible effects of stratified sampling designs.

Results from simulation studies, further theoretical investigations and many different data analyses provide a fairly bleak picture for the use of canonical analysis as an inferential procedure in ecology. The statistical assumptions which insure that the canonical analysis corresponds to posterior classification are almost never met by ecological data. Frequency distributions are almost always non-normal, usually highly skewed, often bimodal, in a great many cases discrete, and covariances are almost universally heterogeneous. The separate and combined effects of these violations on the canonical analysis are almost totally unknown.

Even when the assumptions are met, small sample stability problems arise. Preliminary simulation results by the author indicate considerable instability of the canonical coefficients, due solely to sampling variability. This instability increases rapidly with increases in numbers of variables and groups, and with decreases in sample size and distances between group means. What this means in practice is that any pattern exhibited by the canonical coefficients may be accidental and therefore of no ecological consequence. The effects of sampling variability on the canonical coefficients remain largely unexplored, though the work of Anderson (1963), Rao (1965, 1966) and others provides a theoretical starting point.

Other problems arise when the canonical analysis is based on data gathered by a stratified sampling design. The canonical analysis is sensitive, to a largely unknown degree, to relative as well as absolute sample sizes. This means that decisions concerning relative sampling intensities of groups may have a major impact on the structure of the canonical functions irrespective of the underlying probability structure of the mixture. Such an inherent indeterminancy can undermine any interpretation of the analysis.

There are, in short, a number of more or less serious problms in the application of canonical analysis. That they remain unresolveed at the present time is not an argument to abandon the technique. It does suggest, however, the need for careful planning of studies utilizing canonical analysis, and a healthy scientific skepticism in both the interpretation and the reporting of results.

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DISCUSSION

LESLIE MARCUS: Your approach requires that each sample of the habitat correspond to a unique species utilizing it. In some restricted cases this is appropriate, but in a great many others it is not. More generally there is some probability of use by each of the species, so that a technique like canonical correlation is more appropriate.

KEN WILLIAMS: I agree. The conceptual framework of DA requires the existence of distinct statistical populations and an unambiguous association of sampling units to them. There is a very large number of problems which fit this framework, as indicated in my paper. However, multiple use of sampling units by different species does not. Problems of species-habitat or community-habitat relationships for such cases could better be handled by something like canonical correlation. Another possibility might be to combine correspondence analysis and multivariate multiple regression.

BARRY NOON: There are instances in the literature where principal components analysis (PCA) and discriminant analysis (DA) have been used with the same set of data. How does one interpret differences in ordination loadings?

KEN WILLIAMS: These two procedures focus on different structural features of the data, and address different questions. It is important to recognize this, in order to avoid misinterpretation of the different results. Some confusion about the relationship of PCA and DA probably arises from their mathematical similarities. Both, for example, involve an eigenstructure analysis, and both can be used to assess differences among groups of observations in a space of reduced dimensionality. In the case of PCA the space is defined by the dominant eigenvectors of a covariance (or correlation) matrix, whereas for DA the space is generated from eigenvectors of a matrix involving group means themselves. Nonetheless, both techniques represent a coordinate rotation of multivariate measurements and a reduction of their dimensionality.

The basic difference between them is in the way the group structure is accounted for. DA requires well defined groups, and utilizes this feature by means of the equation

$$[\underline{B} - \lambda\underline{W}]\underline{u} = 0.$$

PCA, on the other hand, uses the data matrix without reference to structure:

$$[\underline{T} - \lambda\underline{I}]\underline{v} = 0$$

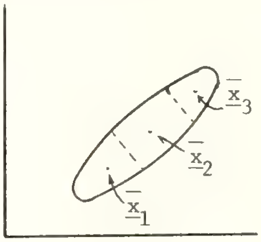
or

$$[\underline{R} - \lambda\underline{I}]\underline{v} = 0,$$

where $\underline{R}$ is the correlation matrix based on $\underline{T}$, and

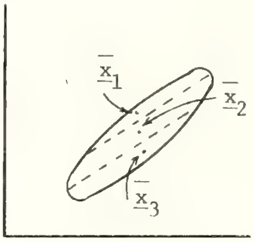
$$\underline{T} = \underline{B} + \underline{W}.$$

Clearly the relationship of axes for PCA and DA depends on differences in structure for $\underline{T}$, $\underline{B}$ and $\underline{W}$. To see how these differences may affect interpretation of the data, consider a partition of data into groups such that the group means lie along the dominant axes of dispersion. In two dimensions this situation appears as:



Then provided $\lambda_i/\Sigma_i \lambda_i$ is close to unity (i.e., the first eigenvector dominates the eigenstructure of T) the principal component $\underline{v}_i = \underline{P}_1' \underline{x}$ and canonical variate $\underline{z}_1 = \underline{u}_1' \underline{x}$ will be approximately the same linear function. Under these conditions the clustering of groups will be displayed in component as well as discriminat space.

Now consider a partition which looks like:



The dominant principal component will not display clustering of groups in this situation, since groups overlap extensively along the dominant axis. DA, however, displays almost total separation of groups along the dominant canonical axis, reflecting the data partition. This difference between principal components and the canonical functions demonstrates that group structure, though highlighted by appropriate linear transforms (the canonical variates), may be completely obscured by others (the principal components).

Thus there is no guarantee that PCA will display important data structures; nor can one conclude a lack of structure based on projections of data in component space. This is not unexpected, since PCA is designed specifically for variance maximization rather than maximum group separation. In fact, every linear transform of observation data gives us a different look at the multivariate system. What one sees depends in large measure on the manner in which he looks, i.e., the transform he uses. PCA provides insight into the components of overall variation for a system, but not necessarily its group structure. DA gives a look at group separation, but not at overall variation. That these two procedures often ordinate in quite different ways therefore should come as no surprise.

THEORY AND METHODS OF FACTOR ANALYSIS AND PRINCIPAL COMPONENTS[1]

Helen Bhattacharyya[2]

Abstract.--A brief discussion is given on the historical development of factor analysis, the kind of data for which factor analysis is applicable, and the kind of result one may obtain. The distinction between principal components analysis and factor analysis is clarified, and the relationship between the unique factors and the communalities in the reduced correlation matrix described. A derivation of the principal components is given, followed by a description of the principal factor solution and interated principal factor solution. Without mathematical details, the concept of maximum likelihood solution is introduced. Once a direct solution is obtained possible rotations, orthogonal and oblique, are discussed as attempts at deriving more conceptually meaningful common factors. The nonuniqueness of factorization of the correlation matrix is shown. The concept of simple structure is introduced and a graphical representation is given illustrating the meaning of rotation of factors. Factor scores and scoring coefficient matrix are described.

Key words: Characteristic equation; characteristic root; communalities; correlation matrix; factor analysis; least squares; maximum likelihood; principal components.

INTRODUCTION

In understanding factor analysis, it helps to know a few things that the procedure does not do. Unlike discriminant analysis, factor analysis does not attempt to distinguish two or more distinct populations. There is no classification problem. Unlike multiple regression, factor analysis does not estimate any relationship between a set of independent variables and one or more dependent variables. The kind of data for which factor analysis is applicable usually consists simply of one sample of multivariate observations. With a sample size N and n variables, the raw data for factor analysis would be of the following form:

Obs.	Z_1	Z_2	. . . . . .	Z_n
1				
2				
.				
.				
.				
N				

where Z_1, Z_2, ..., Z_n denote the n variables measured for each observation. An example of the variables Z_i, $i = 1, \ldots, n$, follows:

Eight Physical Measurements (Harman 1968)

Z_1 = Height
Z_2 = Arm span
Z_3 = Length of forearm

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Z_4 = Length of lower leg
Z_5 = Weight
Z_6 = Bitrochanteric diameter
Z_7 = Chest girth
Z_8 = Chest width.

The primary purpose of factor analysis is to bring about a reduction in dimensionality, to explore relationships among large numbers of observed variables in an effort to find "factors" that reduce the complexity of the situation. In the example, the goal is to find a relatively few underlying common factors such that the eight measurements may be described as a linear function of these common factors.

HISTORICAL BACKGROUND

Spearman (1904) first introduced the concept of factor analysis in an article titled "General intelligence, objectively determined and measured." Early researchers in the field were primarily concerned with finding one common underlying factor, intelligence for example, that would help explain an individual's performance on a variety of different tests. Spearman called this the two-factor theory, one common factor and another specific to a particular test. By the early 1930's it became evident, through the writings of Thurstone (1931) and others, that the two-factor theory was not sufficient to describe a battery of psychology tests. In the 1930's, there developed the concept of multifactor theory; that is, there can be more than just one common factor. The subject of factor analysis, then, is to find the common factors and the relationship between the observed variables and the common factors.

FACTOR ANALYSIS MODEL

Let the observed variables be denoted by Z_1, Z_2, ..., Z_n and the common factors by F_1, F_2, ..., F_m where $m < n$. With the inclusion of the unique factors, U_1, U_2, ..., U_n, the basic linear relationship between variables and factors may be written:

$$Z_1 = a_{11}F_1 + a_{12}F_2 + \dots + a_{1m}F_m + d_1U_1$$

$$Z_2 = a_{21}F_1 + a_{22}F_2 + \dots + a_{2m}F_m + d_2U_2$$

$$\vdots$$

$$Z_n = a_{n1}F_1 + a_{n2}F_2 + \dots + a_{nm}F_m + d_nU_n ,$$

where a_{ij} and d_i, $i=1,\dots,n$, $j=1,\dots,m$, are constants. The matrix $((a_{ij}))$ is called the factor pattern matrix, and an element a_{ij} is called the factor loading of variable Z_i on factor F_j. The unique factors U_i are assumed to be independent of the common factors and independent of each other. For simplicity of exposition, the common factors may be assumed orthogonal to each other, although this is not strictly necessary as will be seen in the discussion of oblique factor rotation. A further assumption is that Z_i, F_j, U_i are all standardized to have mean 0 and unit variance.

Referring to the above example, Z_i would denote the observed variables height, arm span, ..., chest width, so that n=8. The F_j, $j=1,\dots,m$, are the common factors. Prior to performing the factor analysis the common factors and the value of m are assumed unknown. Letting R denote the observed correlation matrix corresponding to the N n-variate observations, the problem is to find a numerical solution for the elements of the pattern matrix $((a_{ij}))$ which would, in some sense, best reproduce R.

PRINCIPAL COMPONENT ANALYSIS

The use of principal components as a data reduction technique was introduced by Pearson (1901) and further developed by Hotelling (1933). The principal component solution will be described first as it avoids some of the inherent difficulties in factor analysis.

Principal Component Model

Let the principal components be denoted as P_1, P_2, ..., P_n. The linear relationship between Z_i, the observed variables, and P_j may be written:

$$Z_1 = a_{11}P_1 + a_{12}P_2 + \dots + a_{1n}P_n$$

$$Z_2 = a_{21}P_1 + a_{22}P_2 + \dots + a_{2n}P_n$$

$$\vdots$$

$$Z_n = a_{n1}P_1 + a_{n2}P_2 + \dots + a_{nm}P_n .$$

The principal components P_j, $j=1,\dots,m$, where m=n, are assumed to be orthogonal to each other and to have variances $Var(P_1) \geq Var(P_2) > \dots \geq Var(P_n)$.

Note that this model differs from the factor analysis model in that m = n and that there are no unique factors. As in factor analysis, the objective is to find the matrix of coefficients $((a_{ij}))$.

Principal Component Solution

Consider the derivation for P_1, the first principal component. Let $P_1 = \underline{a}'\underline{Z} = a_1Z_1 + a_2Z_2 + \dots + a_nZ_n$, then

$$\mathrm{Var}(P_1) = \underline{a}'R\underline{a}, \qquad (1)$$

where R is the covariance matrix of the Z_i's, or equivalently the correlation matrix of the Z_i's if all Z_i's are standardized to mean 0 and unit variance. Although standardizing the Z_i's is not necessary in principal component analysis, this is usually recommended especially when the variables are measured in different scales.

The next step is to maximize $\mathrm{Var}(P_1)$, subject to a normalizing restraint $\underline{a}'\underline{a} = 1$. Using Lagrange multiplier λ and setting to 0 the partial derivatives with respect to a_i,

$$\frac{\partial}{\partial \underline{a}} [\underline{a}'R\underline{a} + \lambda(1 - \underline{a}'\underline{a})] = 0$$

$$2(R - \lambda I)\underline{a} = \underline{0}. \qquad (2)$$

For a nontrivial solution to (2) λ must satisfy the characteristic equation

$$|R - \lambda I| = 0 \qquad (3)$$

The left hand side of (3) is a polynomial in λ of degree n, hence there are n solutions $\lambda_1, \lambda_2, \dots, \lambda_n$. These are called the characteristic roots (or eigenvalues), and corresponding to each λ_i there is a characteristic vector (or eigenvector) $\underline{a}_i$ such that

$$(R - \lambda_i I)\underline{a}_i = \underline{0}.$$

Premultiplying (2) by $\underline{a}'$ gives $\underline{a}'R\underline{a} - \underline{a}'\lambda I\underline{a} = 0$, or $\underline{a}'R\underline{a} = \lambda$. But, $\underline{a}'R\underline{a} = \mathrm{Var}(P_1)$ from (1). Therefore, $\mathrm{Var}(P_1) = \lambda_1$, where λ_1 denotes the largest characteristic root; and $P_1 = \underline{a}_1'\underline{Z}$, where $\underline{a}_1$ is the characteristic vector corresponding to λ_1.

Similarly, the second principal component $P_2 = \underline{b}'\underline{Z}$ may be derived using restriction $\underline{b}'\underline{b} = 1$ and the further restriction $\underline{a}_1'\underline{b} = 0$. However, this is not necessary. If the characteristic roots $\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_n$ are ordered, then the ith principal component is $P_i = \underline{a}_i'\underline{Z}_i$ and $\mathrm{Var}(P_i) = \lambda_i$.

One may ask what has been accomplished. The n variables have resulted in n principal components. No apparent reduction in dimensionality has been achieved if all principal components are kept. However, in defining the principal components, it is hoped that the sum of the m characteristic roots, m < n, would nearly equal n. The sum of the variances of Z_i is $\sum_{i=1}^{n} \mathrm{Var}(Z_i) = n \times 1 = n$ and the sum of the variances of the principal components is $\sum_{i=1}^{n} \mathrm{Var}(P_i) = \sum_{i=1}^{n} \lambda_i = n$. If $\sum_{i=1}^{m} \lambda_i$ is very near n, then the components corresponding to the smaller λ_i, $i = m + 1, \dots, n$, contribute very little to the variation in the Z_i and, hence, may be neglected.

FACTOR ANALYSIS

Recall the factor analysis model given earlier,

$$Z_i = a_{i1}F_1 + a_{i2}F_2 + \dots + a_{im}F_m + d_iU_i,$$

$$i=1,\dots,n,$$

where F_i are orthogonal to each other and independent of U_i,

$$\mathrm{Var}(Z_i) = 1 = \mathrm{Var}\left(\sum_{j=1}^{m} a_{ij}F_j\right) + \mathrm{Var}(d_iU_i).$$

Let $h_i^2 = 1 - \mathrm{Var}(d_iU_i)$. The quantity of h_i^2, $i=1,\dots,n$, is called the communality of Z_i because it represents the variance of Z_i due to the common factors F_j, $j=1,\dots,m$.

In solving for the factor pattern matrix, the object is to find that set of loadings a_{ij} which best reproduces the correlation matrix. Since the variance of Z_i due to the common factors F_j, $j=1,\dots,m$, is h_i^2 rather than unity, it is reasonable then to substitute h_i^2 for unity in the diagonal elements of the correlation matrix. The result is called the reduced correlation matrix and computationally this constitutes the basic difference between the principal component solution and the common factor solution. Note that in principal component analysis the variance of Z_i due to the components is necessarily unity since there is no provision for a unique factor.

Two commonly used methods for estimating the communalities are 1) take h_i^2 to be the square of the multiple correlation coefficient between Z_i and the other n-1 Z's and 2) take h_i^2 to be the largest (absolute value) correlation in each row.

Principal Factor Solution

Once the numerical value of each element including the communalities in the reduced correlation matrix is obtained, the solution for the factor pattern matrix may proceed as with the principal components solution. The characteristic equation is formed and solved for the characteristic roots and characteristic vectors. The reduced correlation matrix for the example is

$$\begin{array}{c|cccccccc}
 & Z_i & Z_2 & Z_3 & Z_4 & Z_5 & Z_6 & Z_7 & Z_8 \\
Z_1 & h_1^2 & & \text{(symmetric)} & & & & & \\
Z_2 & 0.846 & h_2^2 & & & & & & \\
Z_3 & 0.805 & 0.881 & h_3^2 & & & & & \\
Z_4 & 0.859 & 0.826 & 0.801 & h_4^2 & & & & \\
Z5 & 0.473 & 0.376 & 0.380 & 0.436 & h_5^2 & & & \\
Z_6 & 0.398 & 0.326 & 0.319 & 0.329 & 0.762 & h_6^2 & & \\
Z_7 & 0.301 & 0.277 & 0.237 & 0.327 & 0.730 & 0.583 & h_7^2 & \\
Z8 & 0.382 & 0.415 & 0.345 & 0.365 & 0.629 & 0.577 & 0.539 & h_8^2
\end{array}$$

At this point, the question that usually arises is how many factors should be retained. Although under certain normality conditions the statistical significance for the number of factors can be tested, the usual rule of thumb is to keep only those characteristic roots of value greater than unity. This concept is intuitively reasonable since $Var(Z_i) = 1$, and any common factor which accounts for less than unit variance would not be very helpful in achieving parsimony.

A number of other factorization methods are available. Two other methods will be described briefly, the iterated principal factor solution and the maximum likelihood solution.

Iterated Principal Factor Solution

This method may be considered an improved principal factor solution. Beginning with initial estimates of communalities, factor loadings are obtained by the principal factor method. Using the factors extracted, new estimates of communalities are computed and new factor loadings obtained. This iterative procedure is continued until the new communalities differ by less than a predetermined small amount from the previous communalities.

Maximum Likelihood Solution

Although the principal factor solution was well accepted by psychologists and social scientists, there were mathematical statisticians who continued trying to find a solution within the rigorous framework of statistical inference. The breakthrough came when Lawley (1940) developed equations for the maximum likelihood estimation of factor loadings. Although the derivation and algorithms are extremely difficult, the basic concepts involved are those of standard maximum likelihood estimation.

The variables Z_i, $i=1,\ldots,n$, are assumed to follow an n-variate normal distribution, hence the sample covariance matrix follows a Wishart distribution. (Recall in the principal factor solution no assumptions were made on the underlying distribution of the variables Z_i.) The goal is to find the expression for the loadings which would maximize the Wishart density. No assumptions are made about the communalities, but it is necessary to assume the number of common factors. This number, however, may be tested subsequently for goodness of fit using a likelihood ratio test. The maximum likelihood solution for factor loadings has the usual desirable properties of maximum likelihood estimators, such as consistency, asymptotic efficiency, and asymptotic normality. One disadvantage of the method at the present time is that it does not always converge properly depending on the particular data set and the computer package used.

ROTATION OF FACTORS

The ability to describe a set of n variables in terms of m factors implies that the observed data points essentially lie in an m-dimensional space imbedded in the original n-dimensional space. However, there is not a unique set of axes, or factors, for describing this m-dimensional space. It can be shown algebraically that the factorization of the correlation matrix is not unique.

The factor analysis model presented earlier may be written as $\underline{Z} = A\underline{F}$ if we omit the unique factors and use A to denote the n x m pattern matrix. Assuming the common factors to be orthogonal and standardized, the variances and covariances of the standardized variables $Z_i = a_{i1}F_1 + a_{i2}F_2 + \ldots + a_{im}F_m$, $i=1,\ldots,n$, may be denoted as

$$Var(Z_i) = r_{ij} = \sum_{j=1}^{m} a_{ij}^2 \text{ and}$$

$$Cov(Z_iZ_k) = r_{ik} = \sum_{j=1}^{m} a_{ij}a_{kj}$$

so that the correlation matrix of Z_i may be written $R = AA'$. If T is an orthonormal matrix and the transformation $B = AT$ is made, then $BB' = (AT)(AT)' = ATT'A' = AIA' = R$. Factorization of R is not unique since it may be factored into AA' as well as BB'. The question, then, is which factor pattern matrix should be chosen, A or B.

Intuitively, it is obvious that the factor pattern chosen should be the one which leads to conceptually meaningful factors. Thurstone (1935, 1947) gave the following rules which he called simple structure principles for choosing the factor pattern matrix.

1. Each row of the factor matrix should have at least one zero.
2. If there are m common factors, each column of the factor matrix should have at least m zeros.
3. For every pair of columns of the factor matrix there should be several variables whose entries vanish in one column but not in the other.
4. For every pair of columns of the factor matrix, a large proportion of the variables should have vanishing entries in both columns when there are four or more factors.
5. For every pair of columns of the factor matrix, there should be only a small number of variables with non-vanishing entries in both columns.

The ideas embodied in these rules, simplification of the rows and simplification of the columns, were formalized by Carrol (1952), Kaiser (1958), and others and led to the orthogonal and oblique rotations commonly used today.

Quartimax Rotation

This is an orthogonal transformation which attempts to simplify the rows of the pattern matrix. The quantity maximized is

$$Q = \sum_{i=1}^{n} \sum_{j=1}^{m} a_{ij}^{4}. \qquad (4)$$

The name quartimax is applied because a_{ij} is raised to the 4th power. This procedure is equivalent to minimizing Q' where

$$Q' = \sum_{i=1}^{n} \sum_{j<\ell=1}^{m} (a_{ij}a_{i\ell})^{2}. \qquad (5)$$

It is evident from (5) that minimizing Q' simplifies the rows of the pattern matrix. It will be shown now that maximizing Q is equivalent to minimizing Q'.

Since communalities, and hence the squares of communalities, remain constant under orthogonal transformations, we have

$$(\sum_{j=1}^{m} a_{ij}^{2})^{2} = \sum_{j=1}^{m} a_{ij}^{4} + 2 \sum_{j<\ell=1}^{m} (a_{ij}a_{i\ell})^{2} = \text{constant}.$$

Summing over the n variables gives

$$\sum_{i=1}^{n} \sum_{j=1}^{m} a_{ij}^{4} + 2 \sum_{i=1}^{n} \sum_{j<\ell=1}^{m} (a_{ij}a_{i\ell})^{2} = \text{constant}.$$

Since the sum of the two terms on the left hand side is a constant, maximizing the first term is equivalent to minimizing the second term.

Varimax Rotation

This orthogonal transformation attempts to simplify the columns of the pattern matrix. If a simple factor is defined as one with only 0's and 1's in the column, then the varimax rotation attempts to bring about this simplicity by maximizing V_j.

$$V_j = 1/n \sum_{i=1}^{n} (a_{ij}^{2})^{2} - 1/n^{2} (\sum_{i=1}^{n} a_{ij}^{2})^{2},$$

j=1, 2, ..., m, the variance of the squared loadings in each column. Maximizing $\sum_{j=1}^{m} V_j$ results in a rotation overly influenced by the size of the communalities of the variables. In practice, this is taken into account and the quantity actually maximized in the varimax rotations is

$$n^{2}V = n \sum_{j=1}^{m} \sum_{i=1}^{n} (a_{ij}/h_{i})^{4} - \sum_{j=1}^{m} (\sum_{i=1}^{n} (a_{ij}/h_{i})^{2})^{2}.$$

Oblique Rotation

The criterion of simple structure remains as with orthogonal rotations, but the method is no longer limited to orthogonal transformations of the factors. The use of oblique factors is becoming increasingly popular because it affords more flexibility in defining the underlying factors and because computational difficulties are no longer an obstacle with the availability of computer packages. Harman (1968) gives an excellent discussion of several oblique rotation methods.

Graphical Representation

Thurstone's (1935, 1947) simple structure principles may be interpreted graphically as requiring the data points to lie, to the extent possible, on or near the reference axes defined by the factors. Factor rotation then is an effort to rotate the axes to achieve this goal. Figure 1 gives an illustration of orthogonal and oblique rotations for two factors. Data points are denoted by X's. The original factor solution is represented by F_1, F_2, the rotated orthogonal solution by G_1, G_2, and the rotated oblique solution by G_1 and G_2'.

Numerical Example

The factor patterns under different rotations for the example is given in table 1. Two factors were retained in the initial solution. Under all rotations, variables Z_1 to Z_4 loaded heavily on F_1 and variables Z_5 to Z_8 loaded heavily on F_2. An examination of these variables leads us to conclude that Factor 1 is a measure of lankiness and Factor 2 is a measure of stockiness.

FACTOR SCORES

Often the interest in factor analysis does not end in simply being able to obtain the factor pattern and verbalize the factors extracted. Sometimes one may wish to go one step further and find the "observed" values, or scores, of the factors; that is, to describe the factors in terms of the observed variables. This may be useful, for example, in carrying out a regression analysis using m factors instead of the original n variables as the independent variables.

In principal component analysis, the computation of the scoring coefficient matrix is straightforward. In the model $\underline{Z} = A\underline{P}$, the matrix A is square and usually full rank, and the solution for $\underline{P}$ is simply $\underline{P} = A^{-1}\underline{Z}$.

For the factor analysis model,

$$Z = A\underline{F} + D\underline{U}, \qquad (6)$$

where the matrix A is n x m and D denotes the diagonal matrix containing the coefficient d_i of the unique factors, a least squares regression approach is generally used. If $D\underline{U}$ is the error term, then (6) may be considered a linear regression of $\underline{Z}$ on A where $\underline{F}$ are the coefficients. From standard regression theory the least squares solution for $\underline{F}$ is $\underline{F} = (A'A)^{-1}A'\underline{Z}$.

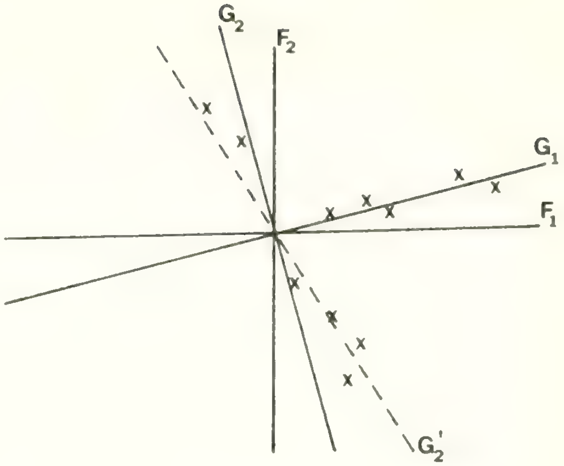

Figure 1. Graphical representation of factor rotation illustrating original factor solution (F_1,F_2); rotated orthogonal solution (G_1,G_2); and rotated oblique solution (G_1,G'_2).

COMPUTER PACKAGES

Computer programs for factor analysis may be found in SAS (Statistical Analysis Systems 1979), SPSS [Statistical Package for the Social Sciences (Kim 1975)], and other statistical packages. Typically, the programs are easy to use and only require a few lines of code. In SAS, for example, the following code would produce a factor analysis using the iterated principal factor method and the varimax rotation on variables Z_1, Z_2, ..., Z_8.

```
PROC FACTOR METHOD=PRINIT ROTATE=VARIMAX SCORE;
     VAR Z1 - Z8;
```

Table 1. Factor patterns for example on eight physical measurements.

	Factor pattern							
	Initial solution		Quartimax rotation		Varimax rotation		Oblique rotation	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Z_1	0.86	-0.33	0.90	0.20	0.88	0.27	0.78	0.05
Z_2	0.85	-0.41	0.93	0.13	0.92	0.21	0.84	-0.03
Z_3	0.81	-0.41	0.90	0.10	0.89	0.18	0.81	-0.05
Z_4	0.83	-0.34	0.88	0.17	0.86	0.25	0.77	0.02
Z_5	0.75	0.56	0.32	0.88	0.24	0.90	-0.00	0.83
Z_6	0.64	0.51	0.25	0.77	0.18	0.79	-0.01	0.71
Z_7	0.56	0.49	0.20	0.72	0.13	0.73	-0.06	0.70
Z_8	0.62	0.37	0.31	0.66	0.25	0.68	0.09	0.57

Output would include the correlation matrix, characteristic roots, the factor pattern matrix, the rotated factor pattern matrix, and the scoring coefficient matrix. To create a new data set containing the factor scores for the original observations, the above code may be modified.

```
PROC FACTOR METHOD=PRINIT ROTATE=VARIMAX
     SCORE OUT=COEFF; VAR Z1 - Z8;

PROC SCORE DATA=OLD SCORE=COEFF OUT=NEW;
```

In this example OLD is the name of the original data set containing the N observations on variables Z_1, Z_2, ..., Z_8, and NEW is the name of the newly created data set containing the N factor scores on the factors F_1, F_2, ..., F_m.

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DISCUSSION

JAMES DUNN: I question the statement that PCA does not assume anything. Certainly the existence of second-order moments, i.e., a covariance matrix, is assumed. It seems nonsense to apply PCA to this if the variances and covariances depend on the mean values, i.e., as in sampling from multivariate Poisson distribtution. But the only distribution in which the covariance matrix is not functionally related to the mean is multinormal.

HELEN BHATTACHARYYA: Principal components and factor analysis are performed on the sample covariance or sample correlation matrix, which always exists with any reasonable data regardless of the existence of the population moments. Classical factor analysis is a method of determining the dimensionality of the data space and does not attempt at statistical inference or tests of hypotheses, procedures for which assumptions on underlying distributions are necessary. There is no disagreement on the assumption of multivariate normal distribution when the maximum likelihood method of factorization is used.

As to the functional dependence of the mean and the variance, surely the variance of a uniform distribution on (c-a, c+a) is not functionally dependent on the mean c.

JAMES DUNN: What is your impression of the usefulness of oblique factor solution in habitat analysis?

HELEN BHATTACHARYYA: Since our interest is in extracting factors that are conceptually meaningful rather than mathematically expedient, there is no reason to limit ourselves only to orthogonal factors.

KEN MORRISON: Is there a reason why you did not mention equamax rotation?

HELEN BHATTACHARYYA: Equamax rotation is somewhat of a compromise between quartimax rotation and varimax rotation and may be considered very desirable. There was no reason why it wasn't mentioned, other than that a number of other rotation methods were also not mentioned.

MICHAEL KINGSLEY: Principal components are known not to be invariant against linear transforms of data. Is factor analysis free of similar quirks?

HELEN BHATTACHARYYA: It is true that PCA when performed on the variance covariance matrix is not invariant under linear transformations of the variables. Factor analysis is performend on the correlation matrix and does remain invariant as correlations remain invariant under linear transformations.

JAMES SKALEY: When using PCA or factor analysis there can be non-linear relationships in the data set along with unequal covariances. The results have been distorted, and we cannot assume the underlying linear model. Are there guidelines for the interpretation of the results from these analysis?

HELEN BHATTACHARYYA: Factor analysis assumes the observed variables may be expressed as a linear combination of the factors. If this is not true then the methodologies described are not appropriate. If factor analysis is performed, I do not believe there can be a general guideline on interpreting the results. For a discussion on nonlinear reduction of dimensionality see R. Gnanadesikan (1977. Methods for statistical data analysis of multivariate observations. John Wiley & Sons, New York, N.Y.).

B. KEN WILLIAMS: Just a comment: there are both scale-free and non-scale-free techniques for deteriming factor loadings. A good description is found in N.H. Timm (1975. Multivariate analysis with applications in education and psychology. Brooks-Cole, Monterey, Calif.).

JAMES HARNER: This is merely a comment. I see a fundamental difference between principal components analysis (PCA) and factor analysis. PCA is simply a rotation of axes to achieve certain criteria, whereas factor analysis is based on a model. Also the question of measurement scale is important in ecology. A PCA can be done by scaling with other means than just using the correlation matrix.

CANONICAL CORRELATION ANALYSIS AND ITS USE IN WILDLIFE HABITAT STUDIES[1]

Kimberly G. Smith[2]

Abstract.--Canonical correlation is the generalized case of multiple regression wherein one attempts to examine interrelationships between two (or more) sets of variables simultaneously. This is accomplished by maximizing the correlation between a composite of variables from one set with a composite of variables from the second set. The statistical assumptions involved are discussed briefly and a geometric representation of the procedure is presented.

A major problem with canonical correlation analysis has been interpretation of results. Cross-validation aids in detection of sample-specific covariation to which canonical correlation is quite sensitive. The test of redundancy offers a method whereby relationships between data sets themselves can be examined rather than relationships between composites of two data sets by calculating the variance of one set that is accounted for by the second set. Selection of variables is critically important; sample sizes should be as large as possible; and jackknifing estimators and use of robust estimators may be helpful.

Canonical correlation analysis has been used most often in the fields of education and psychology. It has met with limited success in phytosociological studies partly because the requirement of linear relationships between variables is too strict. In ecological research, studies have sought to characterize morphological and behavioral data with environmental data. Most animal community studies that have used canonical correlation have suffered from small sample sizes. Canonical correlation analysis seems to hold some promise for wildlife habitat studies, and its use should increase as researchers become more familiar with it. The need for planning and appropriate data collection methods are extremely important.

Key words: Bartlett's test of significance; canonical correlation analysis; cross-validation; jackknifed estimators; ordination; redundancy; robust estimators.

INTRODUCTION

Ecological researchers often collect data on two sets of variables and attempt to elucidate relationships between the sets. The two data sets may have a cause-effect (predictor-criterion) relationship; but, more commonly, one is interested in relating biotic and abiotic factors, e.g., the response of an animal population to a suite of environmental factors along some gradient. Measurements may be from only one area, or encompass data collected simultaneously in several areas. The available statistical options include reporting simple product-moment correlations (r), principal component analysis combining the two sets of variables, or canonical correlation analysis (Barkham and Norris 1970). In most cases, calculating simple correlations is not very informative, and complexity (and usually confusion) increases with the size of the data set. Combining the two data sets into one principal component analysis does not maintain the distinctiveness of the two data sets and is therefore difficult to interpret although it does highlight variables that covary. Canonical correlation analysis, a multivariate statistical technique that attempts to find maximal correlations between two data sets, would appear therefore to hold some promise for wildlife habitat studies. Canonical correlation can also be used as a multiple partial correlation technique (Cooley and Lohnes 1971) and has been employed with limited success as an ordination technique (Gauch and Wentworth 1976).

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Canonical correlation analysis was developed by Hotelling (1935, 1936) to examine the relationships between a set of mental test scores and measurements of performance on the same test subjects, although seeds of the technique can be found in the works of Galton, Edgeworth and Pearson at the turn of the century (see Bryant and Atchley [1975] for historical development and comprehensive bibliography). Because calculations involved are extremely laborious to perform by hand, canonical correlation did not become a widely used statistical tool until the advent of computers and publication of a computer program by Cooley and Lohnes (1962). Other problems that have been associated with the use of canonical correlation are the availability of more familiar techniques; the difficulty of interpreting results; and the tendency of results to be situation-specific and not generalizable (Thorndike and Weiss 1973). Canonical correlation has been applied widely in psychological and educational research, but has seen little use in biological research, despite recommendations (e.g., Dunn 1972, Pielou 1977).

Another reason canonical correlation may have been overlooked in biological research is that often biologists are more interested in explaining variance associated with individual measurements (e.g., through the use of principal component analysis) whereas psychological and educational workers have been more interested in correlational relationships (Rao 1955). In some instances, principal component and canonical correlation analyses will produce similar results (e.g., Cassie and Michael 1968, Gauch and Wentworth 1976); however, differences in results from the two procedures may also be of interest (e.g., Barkham and Norris 1970). Cassie (1969) pointed out the great potential for establishing important correlational relationships in biological research, especially when it is tedious and/or expensive to obtain one of the desired data sets. For example, Cassie suggested it would be easier to monitor water temperature and salinity automatically than to collect and analyze plankton samples. Conversely, it would be easier to collect samples of beach infaunal organisms than to determine particle size distributions of the substrate at many sampling sites. The potential value of establishing correlational relationships in such decision-making processes as environmental impact statements or management programs is obvious.

CANONICAL CORRELATION ANALYSIS

Statistical Assumptions

The usual multivariate statistical assumptions apply to canonical correlation analysis: 1) The covariance matrix must be of full rank (Morrison 1976), i.e., there must be more samples than number of variables in both data sets combined. 2) No singularities can exist within the data matrices, i.e., all rows (or columns) must be independent. Singularities arise when a row (or column) of the data matrix is a linear combination of one or more of the other rows (or columns) (see Gauch and Wentworth 1976). Canonical correlation analysis has no solution when a matrix singularity is encountered. The possibility of singularities in large sets of distributional data may limit the usefulness of canonical correlation as an ordinational technique (e.g., Barkham and Norris 1970).

Two other statistical conditions are usually associated with canonical correlation: a multivariate normal (or multinormal) distribution and linear relationships between variables (see Cassie 1969). The constraint of linear relationships between variables (inherent in any linear model, e.g., principal component analysis) limits the usefulness of canonical correlation as an ordination technique for communities, such as in phytosociological studies (Gaugh and Wentworth 1976), but should not limit use of canonical correlation in situations where correlations along a gradient are of interest. Canonical correlation analysis does not require a multivariate normal distribtuion per se (Morrison 1976), but the closer the data approach normality and linear relationships between variables, the more realistic and more easily interpretable (usually) the relationships between variables will be (Williams 1981). Elsewhere in this volume, Dunn (1981) discusses the use of transformations to arrive at homogeneous variance, an attribute of a multinormal distribution; see also Smith (1977).

Description

Canonical correlation analysis is a technique for finding the correlation between one group of variables, taken as a set, and a second group of variables, also taken as a set, and in many respects is like principal component analysis with two data sets instead of one. More precisely, we are interested in finding linear combinations of variables in each set that have maximum correlation. Several linear combinations of the two sets of original variables are possible and each pair of functions is so determined as to maximize the new correlation, subject to the restriction that new correlations must be independent of previously defined ones (i.e., orthogonal) (Cooley and Lohnes 1962). The following discussion draws heavily on a readable discussion of canonical correlation by Thorndike (1978). For other useful discussions, see Cooley and Lohnes (1962, 1971), McKeon (1965), Blackith and Reyment (1971), Bock (1975), Harris (1975), and Morrison (1976). Gittens (1979) presents an exhaustive review of the use of canonical correlation in biological sciences, with an emphasis on botanical research.

Definitions

An understanding of the following definitions is important for the discussion of canonical correlation. In all examples addressed in this paper, analyses are concerned with two sets of original variables, such as beach organisms and substrate characteristics, for example. Through the use of iterations, new values are found for the original variables that taken together are maximally correlated. These new values are called canonical variates and the canonical correlation is the maximum Pearson product-moment correlation between variates. It is important to remember that the canonical correlation is not between original variables, but between variates calculated from the variables. Weights used to derive variates from variables are called canonical coefficients and should not be confused with canonical factors which are correlations between the original variables and the variates.

Canonical correlations are invariant statistics since, being product-moment correlations, they are unaffected by linear transformations of the variables in either set. Several authors, e.g., Kettenring (1971), have generalized canonical correlation analysis to three or more sets of original variables, but I know of no biological studies where more than two data sets have been used.

Geometric model

Geometrically, canonical correlation can be considered as a measure of the extent to which entities occupy the same relative position in the space defined by each of the data sets (Cooley and Lohnes 1962). For example, Barkham and Norris (1970) stated that their canonical correlation study attempted to measure the extent to which study sites occupied the same relative position in vegetation space as in soil property space.

A geometric representation of canonical correlation is presented in figure 1. A set of original variables, A and B, defining plane 1 comprise data set 1. Data set 2 is composed of variables C and D and defines plane 2. This example of two sets each with two original variables is the simplest canonical correlation situation; if one data set contained only one variable, this would be a multiple regression problem. Canonical correlation analysis will reveal a composite of A and B, in this example a line called 1_c (fig. 1), that is correlated with composite of C and D, line 2_c. Remembering that the objective is to define new values of the original variables that taken together will be maximally correlated, if the correlation between 1_c and 2_c were the highest that could be found for the data sets 1 and 2, lines 1_c and 2_c would be the first canonical variates. The correlations between A and B with 1_c and C and D with 2_c would be vectors of canonical factors. The canonical correlation (R) is the cosine of the angle between 1_c and 2_c, dotted in figure 1. As the angle approaches 0^o, the canonical correlation approaches 1.00. The canonical correlation is usually squared and R^2 is the proportion of variance in the canonical variate of one set that is accounted for by the variate of the other set. Again, the relationship being described is between the variates, not between the original variables themselves.

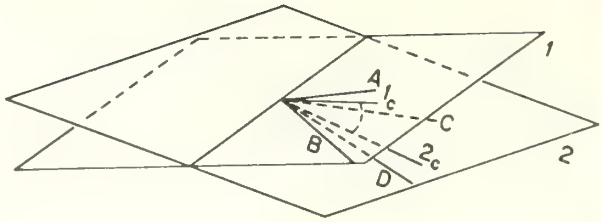

Figure 1. Geometric representation of canonical correlational analysis in two planes A and B. See text for explanation. (from Thorndike 1978)

R^2 is a symmetric index in the sense that the proportion of variance in one set accounted for in the composite of the other set is independent of which set is considered first. In other words, there is no difference in the statistical treatment of the two data sets so that one does not have to make the distinction between a predictor set and criterion or outcome set (Harris 1975).

Test of Significant Roots

As many canonical correlations can be found as there are variables in the smaller set of original variables. Early workers assumed that only the first canonical correlation was important, although this is not always the case. More than the first canonical correlation may be important depending on the question being asked (Cooley and Lohnes 1962). Bartlett (1941-42) developed a χ^2 test that tests the probability that a particular canonical correlation is significantly different from that which would have been expected with random data. The null hypothesis is that the canonical variates derived from one data set are unrelated to the variates of the second data set. Harris (1976) questioned the use of Bartlett's χ^2 test, but Mendoza et al. (1978) challenged Harris's arguments. Lawley (1959) suggested a slight improvement for Bartlett's χ^2 test of significance.

Thorndike (1978) cautioned that statistical significance does not guarantee meaningful biological relationships, a point which may explain many of the interpretational problems researchers have had with canonical correlation. Also, Bartlett's χ^2 test is very sensitive to departures from normality in data (Barkham and Norris 1970). Blackith and Reyment (1971) comment that biologically meaningful combinations may still be present between data sets that have no statistically significant canonical correlations.

Some Solutions To Problems Of Interpretation

Cross-Validation

Some controversy (e.g., Barcikowski and Stevens 1975) has arisen concerning whether one should investigate relationships between weights (coefficients) or correlations between original variables and variates (canonical factors). Coefficients are usually difficult to interpret, if not meaningless (Cassie and Michael 1968), so that most researchers have investigated canonical factors (e.g., Meredith 1964). As pointed out by Poore and Mobley (1980), examining canonical factors has two advantages: 1) species with high correlations with the same canonical variate are grouped together, and 2) environmental variables which have high correlations with the species groupings are elucidated. Usually one would want to consider any factor above 0.50 (e.g., Webb et al. 1973); factors below 0.30 are probably trivial (Cooley and Lohnes 1971). Bock (1975) has suggested using correlations of the variates from one set with original variables of the other set to characterize between set relationships, but I can find no studies that have applied this technique.

The problem of using correlations between original variables and variates is that interpretation becomes dependent upon the specific relationships between measured variables. Situation-specific covariance, such as that arising from the manner in which data were collected, may become a problem so that one cannot generalize the results to other situations. One would, of course, like the covariance to reflect that of the whole population, not just the subset sampled. Thorndike and Weiss (1973) proposed a check of canonical correlation analysis to discover if any abnormalities in the data are a consequence of site-specific covariance (see also Thorndike 1978). Using this technique, called cross-validation, the original data sets are randomly split into two subsets, canonical correlation is performed on one subset, and relationships in the second subset are examined using the weights derived from the analysis on the first subset. If the results within both subsets are similar, then situation-specific covariance is assumed to be minimal. Also, double cross-validation may be performed whereby both subsets are submitted to canonical correlation analysis and both are cross-checked using weights obtained from the opposite analysis. To my knowledge, no one has attempted this procedure with biological data. One needs a fairly large data set to afford the luxury of splitting the data set in half.

Redundancy

From an interpretational point of view, another major problem with canonical correlation analysis is that R^2 represents variance shared by canonical variates and not variance shared between data sets. Thus, canonical correlation cannot be interpreted as correlations between sets of original variables. A strong correlation may be obtained between two canonical variates even though these variates do not extract significant proportions of variance from the respective sets of original variables. To help with this problem of interpretation, Stewart and Love (1968) developed a measure they called redundancy, whereby one can calculate the amount of variance in one set of original variables that is explained by the variate of the other data set. By calculating redundancy for all variates of a data set and summing the results, the proportion of variance of one set that is accounted for by the other set can be calculated. Since the amount of variance of one set explained by another set does not necessarily equal the amount of variance of the second set explained by the first, the measure of redundancy is not symmetrical (as was R^2) and must be calculated for both data sets. Moreover, the first canonical correlation need not and often does not have the highest redundancy. This procedure is thoroughly discussed in Cooley and Lohnes (1971) and Thorndike (1978).

Several biological investigators have used the measure of redundancy recently and use should increase as the technique becomes more well-known. In an investigation of estuarine diatoms, McIntire (1978) found 41% redundancy in species data, meaning that 41% of variation associated with the

26 taxa used could be accounted for by variation in the six environmental variables measured. Likewise, Poore and Mobley (1980) found that 48% of variation in 22 species of marine benthic animals sampled near a sewage treatment plant outwash was associated with variation in nine environmental variables they measured. Note that in both cases, the reverse redundancy calculation, i.e., how much of the environmental variation can be accounted for by the variation in species, is probably meaningless.

In studying dietary relationships among shrubsteppe passerine birds, Rotenberry (1980) found variation in prey size taken could be accounted for by redundancies of only 24% in horned lark (Eremophila alpestris), 28% in sage sparrow (Amphispiza belli), and 38% in western meadowlark (Sturna neglecta). Grouping species data together, redundancy was still about 30%, leading Rotenberry to conclude that the relationship between diet and morphology is more general in nature than other authors have suggested. One would, of course, have expected high redundancy values if morphology and diet were tightly coupled.

Selection of Variables

All too often investigators cannot interpret the factor correlations that appear between environmental and organismal data. Proper selection of variables may help reduce this problem. Variables should be chosen with some a priori knowledge that a relationship exists between the data sets; the ease with which some environmental variables are measured is no reason to assume that they relate to the distribution of organisms of interest. Also, data should be collected specifically for use in canonical correlation analysis rather than using canonical correlation analysis as an ad hoc or a posteriori approach.

In most environmental studies that have applied canonical correlation analysis, the situation has commonly occurred where investigators have measured many variables, but collected few samples. Since the sample-to-variable ratio must be greater than 1 (the greater the better--see section after next), which variables to exclude from analysis becomes important. Thorndike (1978) found that elimination of some variables in most cases did not change the magnitude of the first canonical correlation. He argued that for a given magnitude, the fewer the variables, the greater the likelihood that a canonical correlation is attributable to real population-wide sources of covariation, rather than to situation-specific covariance.

Poore and Mobley (1980) tried three schemes to reduce the number of variables in their marine benthos study. Initially, they eliminated all rare species (average capture < 1 per sample), reducing the total number of species considered from 246 to 49. For the first analysis, they further eliminated all species with less than 118 individuals sampled which reduced the number of species to 22. They found that this procedure produced results that were very difficult to interpret. For the second analysis they deleted all species found in less than half the sampling stations, reducing the 49 species to 18. This procedure eliminated species found only at a few stations, but since they were interested in the subtle influence of sewage on species distributions, this elimination defeated the purpose of the study. For the third analysis, they deleted species correlated with only 1 or 2 of 13 environmental variables measured and also deleted any environmental variables correlated with 6 or less of the 49 species. This left a total of 22 species and 9 environmental variables. This procedure gave the most easily interpretable results since it eliminated both species and environmental variables which were behaving independently of the pattern they were investigating. Care should be used in this procedure, however, since Cassie (1969) found that adding and subtracting variables at random "capriciously" changed values of the corresponding canonical coefficients. In some situations these changes in coefficient values may be desirable, such as in the empirical step-up and step-down procedures discussed in Thorndike (1978).

Plot of Sample Scores

Interpretation of results of a canonical correlation analysis can usually be aided by plotting individual sample canonical scores in a simple two-dimensional plot. Canonical scores are the summation of canonical variates (data for original variables multiplied by canonical coefficients) and are usually available from any canonical correlation computer program. Standardized scores are used in most cases (Morrison 1976:262). One score will be produced for each sample in each data set. For example, in the study of lizard behavior and microclimate discussed later, James and Porter (1979) plotted sample scores from the first canonical correlation with microclimate on one axis and behavior on the other (see fig. 4). In ecological research, as pointed out by Poore and Mobley (1980), the spatial relationship within the sampling stations (or between data points) may be important.

Sample Size

One goal of canonical correlation analysis is the generalization of results to other situations. In order to reach this goal, one must have faith that canonical coefficients and factors actually reflect underlying relationships; stability in estimates of weights and factors should be expected when sample sizes vary. Monte Carlo examinations of weights and factors (Mendoza et al. 1978) demonstrates that the smaller the sample size, the greater the variability in weight and factor estimates. This argues for large sample sizes. Thorndike (1978) suggests as a "rule of thumb" that sample size should be the total number of variables in both matrices squared, plus 100 or so for good measure. He suggests minimal sample size to be 10 times the total number of variables plus 100 for good measure.

Few ecological studies have approached sample sizes of the magnitude suggested by Thorndike. Since individual samples in ecological research usually have greater meaning than test results of anonymous individuals in psychological and educational research (Poore and Mobley 1980), a sample size of three or four times the number of variables is probably adequate in most instances. The inherent problem is that as sample sizes approach the number of variables, the canonical correlation approachs 1.00 and statistical significance of the first canonical correlation is assured. Biological significance, however, should be questioned in such situations and results based only on canonical correlation with equal or near equal numbers of samples and variables should be viewed with skepticism. Although it has been suggested (e.g., Green 1971) that multivariate statistics are still useful when the statistical assumptions are relaxed if the results are biologically meaningful (e.g., see Dueser and Shugart 1979), I would still argue for statistical rigor in the application of multivariate statistics.

A case in point is the study by Herrera (1978), in which an attempt was made to depict differences between non-resident and resident passerine bird species in Spain using six measurements of avian community structure to characterize each group. These measurements were calculated for each month and canonical correlation analysis was used to compare monthly changes in community structure. With only 12 samples (1 per month) and 12 variables (6 for each bird group), Herrera (1978) understandably found a high canonical correlation (1.00), resulting in a linear plot with fall, winter and spring avian communities at one extreme and the summer community at the other (fig. 2). A linear ordination is indicative of a 1.00 canonical correlation, and the high canonical correlation is most probably an artifact of the small sample-to-variable ratio. Herrera (1978) discussed at length differences between resident and non-resident canonical factors, but certainly stability of the canonical factors, as well as the lengthy discussion of their importance must be questioned.

Another example of the sample size problem is the investigation of Aart and Smeenk-Enseink (1975) into the distribution of 12 spider species compared to 17 environmental variables. With only 29 samples, this study also found a canonical correlation of nearly 1.00 and the plot of data points was linear.

Several statistical options are now available for examining stability of coefficient and factor estimates. To reduce bias that may be associated with the estimates, especially when sample sizes are small, jackknifing estimates is appropriate (see Dempster 1966, Miller 1974). This is a procedure (appendix I) whereby the estimates are recalculated, deleting (usually) one sample from each run. Thus, if one had 15 samples total, 15 canonical correlation runs would be made with 14 samples, each time deleting a different sample. A new value for each estimate is calculated based on the sum of the new runs, and a t-test can determine if the new estimates are significantly different from original ones obtained using all samples (appendix I). If there is no significant difference between original estimates and jackknifed estimates, the confidence one places in the estimates is greatly increased. Confidence in results of the Herrera (1978) and Aart and Smeenk-Enseink (1975) studies would have been greatly improved by jackknifing estimates of canonical factors and coefficients.

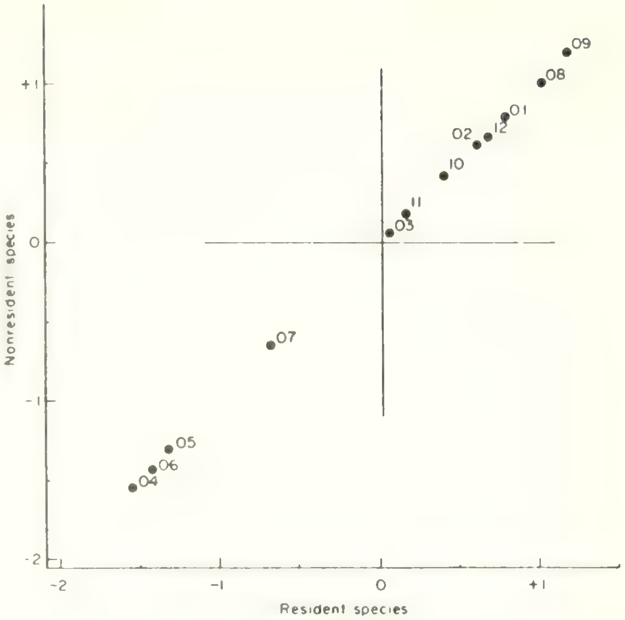

Figure 2. Ordination of 12 monthly samples (e.g., 01 = January) based on canonical correlation analysis (R = 1.00) of resident and non-resident bird communities studied in southeastern Spain. Summer bird communities (April, May, June and July) are separated from other monthly samples. Results are questionable (see text) and linearity of the ordination is due to 1.00 canonical correlation. (from Herrera 1978)

Dempster (1966) suggested that for canonical correlation, deletion of one degree of freedom in each run may be superior to deleting complete samples, which have two degrees of freedom. In the example above, 30 new canonical correlations would be run deleting one sample from one of the two data sets each time, and new values for each estimate would be calculated based on the sum of 30 runs.

To reduce the effect of multivariate outliers (data points that do not appear to be members of the multivariate population under study), canonical correlation using robust estimators can be helpful (Gnanadesikan 1977:127-137). True multivariate outliers can severely affect estimates obtained in most results. Robust estimation decreases, to varying degrees depending on which type of robust estimator is used, the contribution of outlying samples to the estimation of weights (Harner and Whitmore 1981). Gnanadesikan (1977) cautioned that care should be used in the application of robust estimators to small data sets; an apparent "outlier" may in fact only be due to inadequate sampling of the population of interest.

APPLICATIONS OF CANONICAL CORRELATION ANALYSIS

Considering the length of time since development of canonical correlation, the technique has not been applied widely in biological research (see review in Lee [1969]). One of the earliest uses was by Hughes and Lindley (1955) to investigate environmental factors in vegetation trends. Other researchers have attempted to use canonical correlation for phytosociological studies (Austin 1968, Barkham and Norris 1970) but, as mentioned earlier, the use of canonical correlation as an ordinational technique may be limited (Gauch and Wentworth 1976). Webb et al. (1971) found canonical correlation useful in determining the potential of forested areas as agricultural land. Sparling and Williams (1978) suggested the use of canonical correlation for analyzing bird vocalizations, but Martindale (1980) questioned that application.

Correlations Between Morphology and Environment

In animal ecology, some of the most promising applications of canonical correlation have attempted to correlate morphology with some aspect of the environment. In a series of investigations, Jameson and his colleagues used canonical correlation analysis to explore relationships between environmental and morphological variation in the ectothermic Pacific tree frog (Hyla regilla). Since Pacific tree frogs exhibit a wide array of morphological variations which are potentially related to climate and weather through the need to conserve water and energy, canonical correlation analysis was chosen as an appropriate means of depicting the relationships. Calhoon and Jameson (1970) examined relationships between 10 morphological variables and 16 environmental variables that all corresponded to weather patterns the year prior to collection of tree frogs. Tree frogs were collected during one spring from seven different populations in southern California. Discovering that many weather variables were intercorrelated, they performed a second canonical correlation analysis with 8 weather and 10 morphological variables and discussed only the results of the second analysis. Only the first canonical correlation was statistically significant and the results were interpretable as a trade-off between maximizing water conservation by large body size and minimizing heat absorption by small body size. Although not statistically significant, the authors discussed the second canonical correlation as being biologically significant.

In a similar study, Vogt and Jameson (1970) investigated phenotypic variation in one population of Pacific tree frogs sampled monthly over a 3-year period near San Diego, California. In this canonical correlation analysis, 7 morphological measurements of male tree frogs were investigated with 24 environmental (weather) variables covering the 2 years previous to collection of specimens. Five canonical correlations were significant and, taken together, results generally confirm that milder weather correlated with rounder frogs, while decreased rainfall correlated with more elongated animals. Toe length showed the strongest correlation with weather variables suggesting that it responded most rapidly to changes in precipitation. More importantly, canonical correlational analysis elucidated two significant periods in the life of Pacific tree frogs when weather patterns are important: the amount of rain during growth and metamorphosis in spring and the extremes of the high temperatures during fall.

In an expanded version of the two previous investigations, Jameson et al. (1973) examined the relationships of weather patterns, both short- and long-term, to morphological variation in male, female, and juvenile tree frogs from 14 locations in western Oregon. As before, 10 morphological measurements were used and these were correlated to 19 weather variables that characterized weather the year previous to tree frog collection. A second analysis was performed with morphological data using the long-term average (from available weather stations) for the 19 weather variables. The first analysis was termed a "weather" relationship and the second a "climate" relationship. The analyses were performed separately on male, female, and juvenile data sets. The authors concluded that there were meaningful parallels between intraspecific variation and weather and climate. Large males were found in areas of low summer temperatures, but this pattern was not evident in females. Males were more highly correlated with weather patterns, while females were more highly correlated with climatic patterns, a pattern consistent with field observations that males inhabit a more variable microhabitat (ponds). Juvenile morphology was more closely related to weather than climate, presumably because the developmental period they pass through only lasts several weeks. However, the juvenile results were highly variable, suggesting to the authors that there may be selection for variability of response in offspring, a strategy that fecundity of the tree frogs would allow. The major conclusion of this work was that natural selection appears to operate on the size and shape of frogs in different directions during different life history stages and at different localities.

All three tree frog studies illustrate exemplary uses of canonical correlation analysis. Another excellent example is by Boyce (1978) who examined climatic variability and body size in muskrats (Ondatra zibethicus). Results of his analysis are summarized in figure 3. Ten climatic variables were compared with nine morphological measurements and the first canonical correlation was 0.776. (The first six canonical correlations were significant.) Body length (BODY), total length (TOT), condylobasal length (CB) and zygomatic breadth (ZB) were all highly correlated with the first morphological variate and represent body size variation. This is not surprising since the first canonical correlation will almost always be a size-related axis. Longitude (LONG), annual range of evapotranspiration (R_{ev}), and annual coefficient of variation of monthly evapotranspiration (S_{ev}) had high correlations with the climatic variate. Boyce interpreted these results as showing that body size variation is positively correlated with climatic seasonality. Discovering this relationship supported the notion that herbivore body size is positively correlated with primary productivity. Boyce concluded (in part) that the larger individuals may be favored in seasonal environments because they can subsist longer without food.

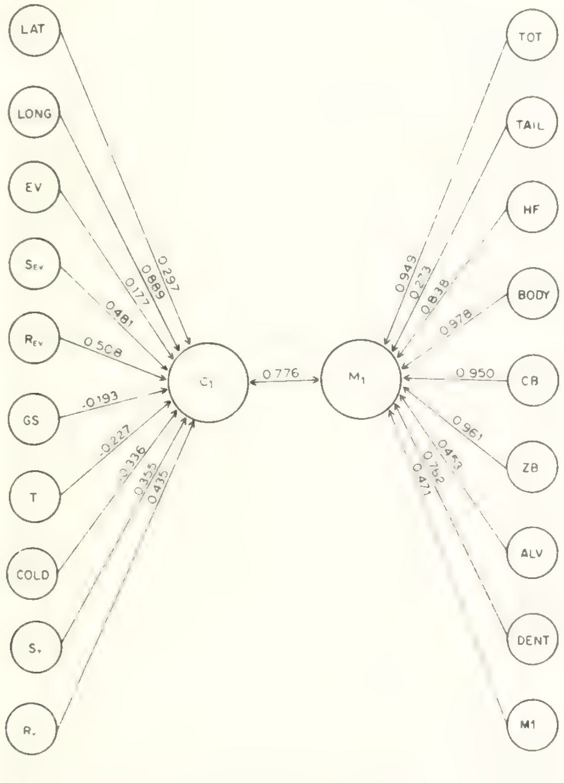

Figure 3. Diagram of the first pair of canonical variates in study of climatic variability and body size variation in muskrats (from Boyce 1978). Definitions of important climatic variables and morphological variables are given in text. C_1 is the first climatic canonical variate, M_1 is the first morphological canonical variate, 0.776 is the canonical correlation, and the numbers along the arrows are correlations between original variables and canonical variate.

Another important study is that of Karr and James (1975) in which 196 species of birds from several continents were compared using 17 morphological measurements and 14 ecological variables, asking the question "What are the ecological correlates of patterns of morphological variation?" The first six canonical correlations were statistically significant and relationships between morphology and ecology became apparent: relatively longer thinner bills and smaller body size (first correlation), relatively longer legs and narrower bills with ground foraging (second correlation), etc. (see Karr and James [1975:table 6] for complete listing). The authors chose to discuss in depth the second canonical correlation since the first correlation related primarily to size phenomena, the results of which were somewhat misleading due to the influcence of the morphologically extreme hummingbirds and sunbirds.

Karr and James (1975) cautioned that care should be used in the selection of variables and generalization of results. They purposely restricted analysis to primarily forest-inhabiting bird species and did not generalize their results beyond that. Addition of, say, water-dependent species such as ducks and herons would have changed the results dramatically (due to the changes in morphology) and the scope of the study would have changed accordingly. Occasionally researchers have combined variables which do not appear to have any apparent relation. For example, DesGrandes (1978) related seven morphological measurements of 21 hummingbird species in Mexico with five ecological variables in order to support his field observations that large birds tend to be sedentary and dominant while smaller species tend to be highly vagile and subordinate. The canonical factors from the first canonical correlation that demonstrate this relationship are presented in table 1. It is unclear what relationship "altitude" has with other variables. Such variables should be culled from canonical correlation analyses and only variables that clearly relate to the same phenomenon should be included in the respective data sets.

Behavioral Applications

A recent paper by James and Porter (1979) demonstrated the applicability of canonical correlation to ecological behavioral investigations. They were interested in relating behavior of the African rainbow lizard (Agama agama) to microclimatic variables. Six microclimatic variables were measured at hourly intervals over several days in October, January, and April and the behavior of a dominant male lizard was also categorized at the same hourly intervals. The authors used canonical correlation

Table 1. Canonical factors associated with first canonical root (R = 0.93) showing relationship between dominance and large body size of hummingbirds contrasted with subordinance and small body size. Data from analysis of Mexican hummingbird communities (DesGrande[3]).

Ecological variables	Factors	Morphological variables	Factors
Dominance	0.92	Length	0.85
Altitude	-0.08	Culmen	0.71
Status	-0.65	Bill width	0.85
Territory	0.40	Bill depth	0.89
Food	0.19	Bill curve	0.14
		Wing disc loading	-0.23
		Dimorphism	0.65

analysis to investigate relationships between behavior and microclimate, and obtained a nice depiction of the effect of heat load on behavior (fig. 4). The distances between columns is a function of the relationship between responses to low (body flattened) and high (body vertical) heat loads. Obtaining the same pattern in October and April argued against a seasonal variation in these relationships.

This work is also important because it employs two methods which improve the usefulness of a canonical correlation analysis. First, although only six microclimatic variables were actually measured in the field, 17 were used in the analysis. These additional 11 variables were constructed by defining various interactions between variables (see James and Porter [1979] for details). The technique of building interactions into the model is used widely in multiple regression, but few workers have considered applying it to canonical correlation analysis.

The second improvement concerns the removal of singularities. Since behavioral data are mutually exclusive, i.e., a lizard cannot be doing two behaviors at the same time, all behavioral rows add up to the same value (1 since all data were categorized). Therefore, the behavior "resting" was eliminated from the analysis so that the sum of the rows was now different. The elimination of one column of data does not affect the conclusions, and in this case, removed the singularity.

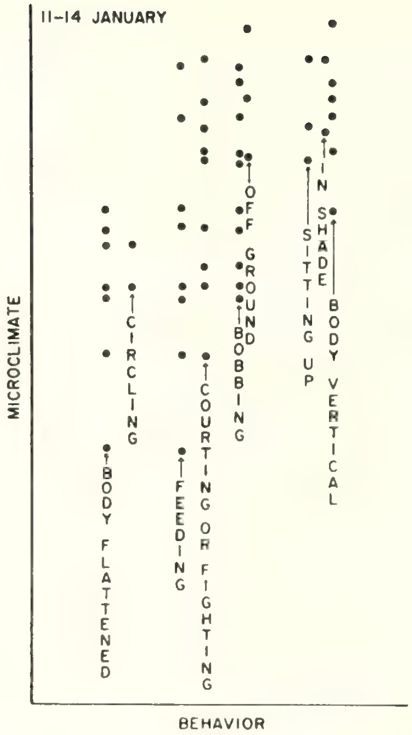

Figure 4. Representation of the relationship between microclimate and behavior of the African rainbow lizard based on canonical correlation analysis (R = 0.72) of data collected between 11-14 January 1971 in Ghana (from James and Porter 1979). Ordination depicts behavioral changes as heat load increases. Each point represents an hourly measurement of behavior and microclimate.

Animal Community Ecological Applications

Using canonical correlation analysis, Webb et al. (1973) were able to present a land-use scheme for nature conservation in Australia based on vegetational characteristics and bird communities of tropical forests. Few other studies have used canonical correlation analysis in terrestrial community ecology, and most that have, suffered from small sample-to-variable ratios (e.g., Herrera 1978).

Use of canonical correlation analysis is increasing in marine ecological studies, which is understandable since specific environmental factors enter prominently into the distribution of many marine invertebrates. One of the first applications was by Cassie and Michael (1968) in a study of invertebrate distribution and sediment size on an intertidal mud flat near Auckland, New Zealand. They were interested in the relationship between eight invertebrate species and nine sediment variables sampled at 21 locations. The analysis suffered from a small sample to variable ratio, and the authors obtained much better results with principal component analysis for which they had 40 samples. But, realizing the sample-to-variable ratio problem, they suggested that canonical correlation analysis may still be useful in larger studies.

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[3] Personal communication with J-L. DesGrandes, Canadian Wildlife Service, Quebec Region, Ste-Foy, Quebec, Canada.

Two recent studies have been more successful with canonical correlation analysis. McIntire (1978) investigated distribution of 26 non-planktonic diatom taxa based on six environmental variables in an estuary on the Oregon coast. The first canonical correlation (R=0.98) ordinated the species along a salinity gradient. The second canonical correlation (R=0.95) highlighted mean daily salinity range and mean temperature, which McIntire interpreted as a gradient to salt tolerance (stenohaline to euryhaline species). In Victoria, Australia, Poore and Mobly (1980) used canonical correlation analysis to ordinate 22 benthic invertebrate species based on nine environmental variables measured at 36 stations at the outwash of a sewage treatment plant. Although the sample-to-variable ratio was small, the authors still found useful results. The first canonical correlation (R=0.99) reflected a depth gradient based primarily on amount of fine sand associated with shallow waters. The second canonical correlation (R=0.98) separated the middle samples from the shallow and deep water samples (figure 5). Such a "horseshoe-shaped" ordination is to be expected when attempting to ordinate species distributions along a steep gradient (e.g., see Phillips [1978]).

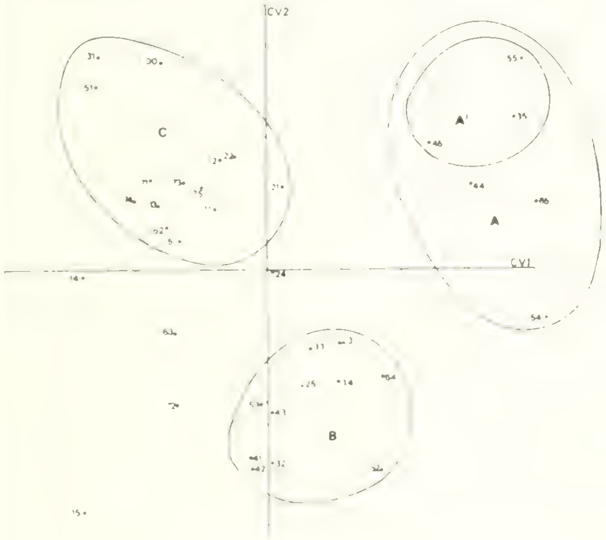

Figure 5. Ordination of benthic marine samples from outwash of sewage treatment plant based on first two canonical variates (CV1 and CV2) (from Poore and Mobley 1980). Separation is along depth gradient: A' = very deep samples, A = deep samples, B = intermediate depths, and C = shallow water samples (ellipses drawn by eye). Placement of some sample stations outside of ellipses (e.g., 14, 72, and 63) is due to unusual environmental conditions at those sites (see Poore and Mobley 1980 for details).

CONCLUSIONS

The major point that researchers who use canonical correlation should keep in mind is that the larger the sample-to-variable ratio, the more stable canonical factors and weights become, so that sample sizes should be as large as possible. As relationships between variables approach linearity and data sets approach a multivariate normal distribution, results should become more easily interpretable.

By perusing the works that have successfully used canonical correlation to date, it becomes clear that experimental design and planning are critical. It is imperative that data be collected with canonical correlation in mind. All too often application of multivariate statistics appears to be an ad hoc or a posteriori approach rather than the a priori approach that it should be. The selection of variables is extremely important and much of the past troubles with interpretation may relate to researchers having no idea how the environmental variables measured actually influence the organism(s) of interest. The problem of adequate sample size may make use of the technique prohibitive, although this has rarely stopped anyone yet!

With proper planning, canonical correlation analysis can become a very useful tool for wildlife habitat studies, and probably will become more widely used as researchers become familiar with it. Planning is certainly the key to successful use and cannot be stressed too heavily.

ACKNOWLEDGMENTS

Frances James kindly read an early draft of this paper and made many helpful suggestions concerning terminology and explanations of examples used in the text. Through her creative use of multivariate statistics, including canonical correlation analysis, she has made great contributions in ecological research and continues to be a leader in the field of applying multivariate statistics to ecological problems.

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APPENDIX I

Jackknife estimation

(written by James E. Dunn)

$\hat{\theta}$ = usual estimate based on all data

Divide data set at random into g groups of h observations each, e.g., typically g = n, h = 1.

Compute $\hat{\theta}_{-i}$, i.e., usual estimate with ith group deleted, $i=1,2,\ldots,g$

Compute pseudo values $\tilde{\theta}_i = g\hat{\theta} - (g - 1)\,\hat{\theta}_{-i}$

$i = 1,2,\ldots, g$

Jackknifed estimate is

$$\tilde{\theta} = \frac{1}{g} \sum_{i=1}^{g} \tilde{\theta}_i$$

$$s^2_{\tilde{\theta}} = \widehat{\mathrm{VAR}[\tilde{\theta}]} = \sum_{i=1}^{g} \frac{(\tilde{\theta}_i - \tilde{\theta})^2}{g-1}$$

Test of significance: $H_o : \tilde{\theta} = \theta_o$

$$t = \frac{\tilde{\theta} - \theta_o}{s_{\tilde{\theta}}/\sqrt{g}} \sim t_{(g-1)}$$

DISCUSSION

JAKE RICE: In your talk you stressed that canonical correlation was exactly that: a correlation method, and one does not need to identify predictor and criterion sets of variables. Suppose you did have some biological reason for identifying one set of variables as predictors and the other set as criteria variables (as is common in simple regression studies); would (or could) one do anything different that might improve the findings? (As in some contexts regression methods provide results preferable to correlation methods on the same data set.)

KIMBERLY SMITH: James Dunn has an answer to that question.

JAMES DUNN: If SAS PROC GLM is available, write a MODEL statement with the criteria variables on the left and the predictor variables on the right. MANOVA mode will work equally well if the predictors are continuous or categorical. In the former, it may be necessary to arrange the MODEL statement properly, specify Type I SS, and accumulate the derived number of H matrices into a composite H_c before computing a likelihood ratio test based on

$$\ln \left(\frac{|E|}{|E + H_c|} \right)$$

or a union-intersection test based on max $\mathrm{ch}(E^{-1}H_c)$.

JOSEPH FOLSE: In multiple regression analysis, inclusion of extraneous variables does not bias other regression estimates whereas deletion of important variables does. What effects does this have in canonical correlations?

KIMBERLY SMITH: One way that has been suggested of attempting to improve canonical correlations is to eliminate variables that have low loadings (or weights) and repeat the analysis with the reduced model. Interestingly, Cassie (1969) has suggested, however, that if one starts to delete variables randomly, the relationships obtained from canonical correlation change rather capriciously. Thus, the same relationship appears to hold true for canonical correlation - inclusion of extraneous variables should not bias other correlation estimates, whereas deletion of important variables will.

DATA-BASED TRANSFORMATIONS IN MULTIVARIATE ANALYSIS[1]

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Abstract.--Univariate transformations are considered initially, because of the common practice of transforming separately the marginal distribution of each variable of a multivariate observation. Familiar examples include those based on a priori assumptions about the underlying sampling distribution, as well as several general classes of empirical transformations recommended in a recent text by Mosteller and Tukey. Multi-normal criteria are considered as a basis for obtaining and evaluating multivariate transformations, including the likelihood criterion and various transformations to uniform statistics. The extension of power and shifted-power transformations to multivariate analysis is reviewed in detail, including recently published work involving q-sample problems.

Key words: Multivariate; power transformation; uniform statistics.

INTRODUCTION

At first exposure, a student without data typically will be intimidated by the wilderness which exists in the world of data transformations. "How," he will ask, "can I interpret a significant difference between means of logarithms of my data?" With data he will seem perfectly comfortable in comparing mean pH values ($-\log H^+$). When life testing with an automatic termination date, say, after 15 days, he will automatically compare means of reciprocal response times, where 'starter' values of 1/16 are routinely assigned for any survivors. An arbitrary error of at most 1/16 for any survivor seems perfectly acceptable in this context. If asked to compare the means when sampling from two populations whose variances clearly are unequal, he will agree that any comparison is ambiguous until a common metric (σ) is established through use of a variance stabilizing transformation.

Even though this manuscript is directed toward multivariate problems, univariate transformations are considered initially because of the common practice of transforming the marginal distribution of each variable separately. Even though marginal normality does not guarantee multivariate normality, as may be demonstrated in rather contrived examples, numerous cases have occurred where this approach has seemed sufficient.

Multivariate transformations are introduced in the following section in the natural language of matrix notation. Capital letters are used to denote matrices (e.g., A, I, Σ), lower case letters underscored for column vectors (e.g., $\underline{y}$, $\underline{j}$, $\underline{\beta}$), and lower case letters in general for scalars, either random variables or constants, including the elements of vectors and matrices.

A natural danger in a paper of this type is to focus on the taxonomy rather than the systematics (ecology) of transformations. To avoid this, I have tried to emphasize what I consider in the process of selecting a data-based transformation.

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In the interest of space, two interesting categorical response situations can only be mentioned here. The *GSK model* (Grizzle, Starmer, and Koch 1969) for analysis of categorical response using linear models has promise for studying multivariate relative frequency problems, such as bird counts by species at different locations, or stomach contents by taxonomic group. Dunn and Cappy (1979a, 1979b) have studied the problem of invertible transformations in this context. The *multivariate logistic model* $p = [1 + \exp(-\underline{\beta}'\underline{x})]^{-1}$ has come into focus as a robust classifier compared to multi-normal classification functions (cf. Efron 1975, Press and Wilson 1978). In particular, it lends itself to use of categorical response variables and non-linear boundaries.

UNIVARIATE TRANSFORMATIONS

Even though the material in this section is generally known, it is reviewed here for completeness. If $y \backsim N(\mu, \sigma^2)$, then it is evident from the uniqueness of the cumulant generating function $K_y(t) = \mu t + \sigma^2 t/2$ that the normal distribution is the only possible distribution in which the mean and variance are functionally unrelated. Since most of our familiar hypotheses tests (e.g., t, F, χ^2, etc.) depend on the normality assumption, finding a transformation of non-normal data whose variance is unrelated to the mean seems to be a logical approach to normalization.

Variance Stabilization From A Priori Assumptions

Suppose that y has mean μ and variance $\sigma^2(\mu)$, and we require a transformation $t = t(y)$ such that var[t] is a constant c to some acceptable order of approximation. Using the familiar stochastic Taylor's series expansion of t(y) about μ leads to the well-known defining equation (cf. Rao 1952)

$$t(\mu) = \int \sqrt{c/\sigma^2(\mu)}\; d\mu \quad . \tag{1}$$

For example, suppose that y has a Poisson distribution with $\mu = \lambda$ and $\sigma^2(\mu) = \lambda$.

Then

$$t(\lambda) = \sqrt{c} \int \lambda^{-1/2}\, d\lambda = 2\sqrt{c}\,\sqrt{\lambda} = \sqrt{\lambda} \ ,$$

provided we specify the approximate variance to be $c = 1/4$. In actual fact if $t = \sqrt{y}$, then $\mathrm{var}[t] = 1/4 + 3/(32\lambda) + (\cdot)/\lambda^2 + \ldots = 1/4 + O(1/\lambda)$. Anscombe (1948) produced a still more stable transformation $t = \sqrt{y + 3/8}$ with $\mathrm{var}[t] = 1/4 + O(1/\lambda^2)$. Clearly, variance stabilization is more effective for Poisson counts with large rather than small means. Familiar transformations, including improvements suggested by Anscombe (1948) appear in table 1. They are data-based in the sense that they reflect our prior beliefs about the parent population being sampled.

A Data-Based Power Transformation

Suppose that y is sampled from a population with mean μ and $\sigma^2(\mu) = \alpha\mu^b$, i.e the variance is proportional to some unknown power of the mean. Using equation (1), one obtains the result

$$t(\mu) = \sqrt{c/\alpha} \int \mu^{-\beta/2}\, d\mu$$

$$= \begin{cases} \mu^{1-\beta/2} \text{ with } c = \alpha(1 - \beta/2)^2 \text{ if } \beta \neq 2 \\ \ell n(\mu) \text{ with } c = \alpha \text{ if } \beta = 2. \end{cases}$$

If a sample is available from each of q populations, or if a large sample from a single population is divided at random into q subsamples, then one may estimate β from the sample means and variances $\{(\bar{y}_i, s_i^2):i=1,\ldots,q\}$ as the slope of the regression of $\ell n\,(s_i^2)$ on $\ell n\,(\bar{y}_i)$. Then $t = \ell n(y)$ or $t = y^{1-\hat{\beta}/2}$, depending on the proximity of $\hat{\beta}$ to 2.

Mosteller-Tukey Transformations

Mosteller and Tukey (1977) approach the problem of selecting a transformation using only prior knowledge that certain parts of the range of t(y) should represent a differential shrinkage or expansion of the domain of y. Selecting a proper transformation is visualized to be an evolutionary process, i.e., try, look, and try again, with interactive access to the data set assumed. Visual display, to look for linear trend or parallel trends, is important to see if progress is being made in the sequence of steps. General families of transformations suggested by Mosteller and Tukey (1977) are summarized in terms of the scale of measurement required. Most readers will feel at ease with their use of 'starter' values t(y + c), though justification of the recommended c = 1/6 is somewhat mysterious.

Amounts and counts. Assuming that $y \geq 0$, one may use

$$t(y) \quad = \begin{cases} A(y/A)^p/p + (1 - 1/p)A \text{ if } p \neq 0 \\ A\,\ell n(y/A) + A \text{ if } p = 0 \end{cases}$$

if a match $t(y) = y$ is required when $y = A$. A choice of $p > 1$ will cause expansion of the tails of the t axis, with the converse holding for $p < 1$. If the data contain zeros, then use of $t(y + 1/6)$ is suggested.

Table 1. Familiar univariate, variance-stabilizing transformations.

Distribution/Mean/Variance	t	var[t]
Poisson/λ/λ	$\sqrt{y + 3/8}$	$1/4 + O(1/\lambda^2)$
Binomial/np/np(1-p)	$\sin^{-1}\sqrt{(y + 3/8)/(n + 3/4)}$	$(4n + 2)^{-1}$
	where n must be a constant.	
Negative binomial/ m/m(1 + m/k)	$\sinh^{-1}\sqrt{(y + 3/8)/(k - 3/4)}$, $k \geq 2$	$\psi(k)/4$
	$\ln(y + k/2)$, $k < 2$	$\psi(k)$
	where k must be known.	
s^2 (Normal population)/ $\sigma^2/(2\sigma^2/(n-1))$	$\ln(s^2)$	$2/(n-1)$
	where n must be a constant.	

Counted fractions. The typical situation is "y successes in n trials". If a started fraction is defined to be

$$f = (y + 1/6)/[y + 1/6) + (n - y + 1/6)]$$

$$= (y + 1/6)/(n + 1/3),$$

then either the folded square root (froot)

$$t(y) = \sqrt{2}(\sqrt{f} - \sqrt{1 - f})$$ or the folded logarithm (flog)

$$t(y) = 1/2 \ln f - 1/2 \ln(1-f) = \ln\sqrt{f} - \ln\sqrt{1-f}$$

$$= 1/2 \ln(y + 1/6) - 1/2 \ln(n - y + 1/6)$$

is recommended. Note that $f = 1/2$ and $t = 0$ in either case when $y = n/2$. Hence, a 50% response corresponds to a symmetry point for t, with little differential expansion in the neighborhood of $t = 0$ and considerable expansion in either tail.

Ranks. If n objects are assigned ranks $r_1,\ldots,r_n$, then the counted fraction transformation may be applied as

$$t_i = 1/2 \ln[(r_i - 1/3)/(n + 1 - r_i - 1/3)]$$

$(i=1,\ldots,n)$.

Alternatively, 'rankits' variously defined as

$$t_i = \begin{cases} \Phi^{-1}\ [(r_i - 1/3)/(n + 1/3)] & \text{(Tukey)} \\ \Phi^{-1}\ [(r_i - 3/8)/(n + 1/4)] & \text{(Blom)}(i=1,\ldots,q) \\ \Phi^{-1}\ [(r_i/(n + 1)] & \text{(Vander Waerden)} \end{cases}$$

are also commonly used in this context (cf. SAS 1979), where Φ is the standard normal cumulative distribution function (c.d.f.).

Grades. Here, the observations are simply classifed into one of q mutually exclusive, but ordered classes $a_1, a_2,\ldots,a_q$. Suppose that the observations are to be scored in terms of an assumed standard distribution with c.d.f. F(y). If the relative class frequencies are $p_1, p_2,\ldots,p_q$ $(\sum_{j=1}^{q} p_j = 1)$, and $s_i = \sum_{j=1}^{i} p_j$, then cut-points are defined by $c_0 = -\infty$, $c_q = \infty$ and $c_i = F^{-1}(s_i)$ for $i=1,\ldots,q-1$. The score μ_i to be assigned to an observation in the i'th class is the conditional mean of the standard distribtuion on the interval (c_{i-1},c_i), that is

$$\mu_i = \int_{c_{i-1}}^{c_i} y \ dF(y)/p_i \quad (i=1,\ldots,q).$$

In the normal case with $F(\cdot) = \Phi(\cdot)$, this becomes

$$\mu_i = [\exp(-c_{i-1}^2/2) - \exp(-c_i^2/2)]/p_i\sqrt{2\pi},$$

(cf. Kendall and Stuart 1967), while for the logistic as the standard distribution, Mosteller and Tukey (1977) give

$$\mu_i = [h(s_i) - h(s_{i-1})]/p_i,$$

where $h(s) = s \ln(s) + (1 - s)\ln(1 - s)$. Note the attractive feature that $c_1,\ldots,c_q$ need not be obtained explicitly in the latter case. In any case, considerable time generally will be required to complete the data recoding in multivariate applications. Cockrell (1980) will distribute (on request) a SAS procedure RECODE which seems to fit this application quite nicely.

MULTIVARIATE TRANSFORMATIONS

In a search for a class of generally useful transformations of a univariate response y, Box and Cox (1964) proposed the power transformation

$$y^{(\lambda)} = \begin{cases} (y^{\lambda} - 1)/\lambda & \text{for } \lambda \neq 0, \\ \ell n(y) & \text{for } \lambda = 0, \end{cases} \qquad (2)$$

provided y > 0, or the shifted-power transformation

$$y^{(\lambda)} = \begin{cases} [(y + \xi)^{\lambda} - 1]/\lambda & \text{for } \lambda \neq 0 \\ \ell n(y + \xi) & \text{for } \lambda = 0, \end{cases} \qquad (3)$$

for $y + \xi > 0$, where ξ either may be a starter value supplied by the user or else treated as an additional parameter to be estimated. Since typical statistics such as t and F are invariant with respect to changes in location and scale, use of $y^{(\lambda)}$ is identical to use of y^{λ} or $(y + \xi)^{\lambda}$, thus equivalent to the power transformation derived above. The particular form of $y^{(\lambda)}$ simply emphasizes the fact that $\ell n(y)$ is a continuity point of $y^{(\lambda)}$ at $\lambda = 0$, that is

$$\lim_{\lambda \to 0} y^{(\lambda)} = \lim_{\lambda \to 0} (y + \xi)^{\lambda}\, \ell n(y + \xi) = \ell n(y + \xi).$$

If $\underline{y}' = (y_1, \ldots y_p)$ is a p-variate response vector, then Andrews et al. (1971) suggested a multivariate extension by defining $\underline{y}^{(\lambda)} = [y_1^{(\lambda_1)}, \ldots, y_p^{(\lambda_p)}]'$, where $y_k^{(\lambda_k)}$ is defined by equations (2) or (3) in terms of parameter sets $\{\lambda_k\}$ or $\{\lambda_k, \xi_k\}$ for $k = 1, \ldots, p$.

In order to choose 'best' values for either of the above parameter sets in any particular application, we must specify our criteria. First, since almost all multivariate analyses depend on statistics which are functions of the covariance matrix, (e.g., principal components, canonical correlation, discriminant functions, and multivariate classification), we shall want a transformation to new variables whose covariance matrix contains all of the information about inter-relationships among the variables (independently of the mean). Again, considering the uniqueness of the cumulant generating function $K_{\underline{y}}(\underline{t}) = \underline{\mu}'\underline{t} + \underline{t}'\Sigma\underline{t}/2$ for $\underline{y} \backsim N(\underline{\mu}, \Sigma)$, this suggests that any criteria for the transformation be based on a characterization of multi-normality. Two of these possibilities are considered in the remainder of this section. Second, since the development of a transformation is likely to be an iterative process, we shall require an easily comprehended measure of our progress toward the optimum and an assessment of our final result. Finally, since in most applications, the original scales of measurement are meaningful, only coordinate dependent approaches will be considered here [cf. Cox and Small (1978) for coordinate independent approaches].

Likelihood Criterion

Let us consider the general q-sample ($q \geq 1$), multivariate case [which includes the q-sample, univariate case discussed by Box and Cox (1964), and the one-sample, multivariate case treated by Andrews et al. (1971)]. Suppose that a random sample $\underline{y}_{i1}, \ldots, \underline{y}_{i,n_i}$ of size n_i is drawn independently from each of q, p-variate populations ($i=1,\ldots,q$). Considering the simpler case of the transformations defined by equation (2), we shall want to find an estimate of the parameter set $\{\lambda_k\}$ such that

$$\underline{y}_{ij}^{(\lambda)} \backsim N(\underline{\mu}_i, \Sigma), \text{ where} \qquad (4)$$

$$(\underline{y}_{ij}^{(\lambda)})_k = (y_{ijk}^{\lambda_k} - 1)/\lambda_k$$

for $i=1,\ldots,q$; $j=1,\ldots,n_i$; and $k=1,\ldots,p$. The requirement of covariance matrix stabilization, $\Sigma_1 = \ldots = \Sigma_q = \Sigma$ (Σ unspecified), as well as normalization seems realistic in light of the usual multivariate procedures. Following Dunn and Tubbs (1980), the joint likelihood for the data set $\{\underline{y}_{ij}\}$ can be re-expressed as the concentrated likelihood function

$$L(\lambda_1, \ldots, \lambda_p) = \exp(-np/2)(n/2\pi)^{np/2} \Phi(\lambda_1, \ldots, \lambda_p)^{-n/2}, \qquad (5)$$

where

$$\Phi(\lambda_1, \ldots, \lambda_p) = |G| / (\prod_{k=1}^{p} \lambda_k \dot{y}_k^{\lambda_k - 1})^2, \qquad (6)$$

$$G = \sum_{i-1}^{q} \sum_{j=1}^{n_i} (\underline{z}_{ij} - \underline{z}_i)(\underline{z}_{ij} - \underline{z}_i)'$$

$$\underline{z}_{ij} = (y_{ij1}^{\lambda_1}, \ldots, y_{ijp}^{\lambda_p})',$$

$$\underline{z}_i = n_i^{-1} \sum_{j=1}^{n_i} \underline{z}_{ij},$$

$$\dot{y}_k = (\prod_{i=1}^{q} \prod_{j=1}^{n_i} y_{ijk})^{1/n} \qquad (k = 1, \ldots, p).$$

Dunn and Tubbs (1980) have successfully applied the Fletcher-Powell conjugate gradient algorithm to obtain an iterative minimization of (6) with respect to $\{\lambda_k\}$, equivalent to maximizing (5), using a FORTRAN IV program locally known as VARSTB. Elements of the required gradient vector

$\nabla\Phi(\lambda_1,\ldots,\lambda_p)$ are given in that paper.

Example. Fisher's classical iris data (1936) consists of 50 observations from each of three varieties of iris, virginica, versicolor, and setosa. Each experimental unit consists of measurements of sepal length and width and petal length and width. This data is often used to illustrate classification and discriminant functions, implicitly assuming equality of the covariance matrices. If a check is performed, Bartlett's test gives $\chi^2 = 144.0$ with 20 degrees of freedom ($P < 0.0001$). VARSTB, on an IBM 370/155, converged to estimates $\hat{\lambda}_1 = -0.43054$, $\hat{\lambda}_2 = 0.51697$, $\hat{\lambda}_3 = 0.39843$, and $\hat{\lambda} = 0.55468$ in three iterations, requiring 47.02 seconds, starting with all exponents identically one. At convergence, the maximum stress between successive iterations was 3.3×10^{-14}. Retesting the transformed values, Bartlett's statistic was reduced to $\chi^2 = 65.2$. Even though still $P < 0.0001$, the reduction of Bartlett's statistic implies that the transformations have been effective. The necessity for transformations is substantiated by testing H_0: $\lambda_1 = \lambda_2 = \lambda_3 = \lambda_4 = 1$, using the generalized likelihood ratio test

$$\begin{aligned}\chi^2 &= n \ \ell n[\Phi(1,1,1,1)/\Phi(\hat{\lambda}_1,\hat{\lambda}_2,\hat{\lambda}_3,\hat{\lambda}_4)] \\ &= 150 \ \ell n[1.5497 \times 10^4/1.30735 \times 10^4] \\ &= 25.51 \text{ with 4 degrees of freedom}\end{aligned}$$

($P<0.00005$). The effectiveness of the transformation will be examined further in a later section.

In summary, this procedure seems to satisfy the three criteria very well. It is based on the multi-normal likelihood function whose covariance matrix is independent of the mean (homoscedastic in the q-sample case). We may observe the decrease of Φ to its minimum in successive iterations, each step automatically determined by the last, and test the effectiveness of the proposed transformations at the end. Finally, the identities of the original variables are maintained, since each is simply raised to some power followed by a shift of location and a change in scale. Jackknifing is a logical means of examining the stability of the estimated powers as well as improving their robustness. Available computer time may become a limiting factor, however, if extensive jackknifing is attempted.

TRANSFORMATIONS TO UNIFORM (U) STATISTICS

Because of their simplistic distributional properties, transformations to uniform (U) statistics have universal appeal. Gnanadesikan (1977) summarized a variety of graphical methods for assessing marginal and joint normality, based on approximate transformations to i.i.d. U statistics. The exactness of his procedures will always be suspect, however, in that no compensation is made for replacing true mean vectors and covariance matrices by sample estimates. O'Reilly and Quesenberry (1973) demonstrated that by conditioning on sufficient statistics, the conditional distributions of a properly transformed subset of the original variables are exactly i.i.d. uniform, U(0,1). Because their results show the most promise due to their exactness and because they are scattered through a relatively recent literature, they are detailed here so far as they apply to assessing both marginal and joint normality in single and q-sample problems. The actual transformations are considered first, followed by a consideration of omnibus means of assessing uniformity. Since it will be required so frequently in the remainder of this section, let $G_\upsilon(\cdot)$ denote the cumulative distribution function (c.d.f.) of student's t distribution with υ degrees of freedom.

One-sample univariate. Suppose that $y_1,\ldots,y_n$ are i.i.d. $N(\mu,\sigma^2)$, and let $\bar{y}_r = \sum_{j=1}^{r} y_j/r$ and $s_r^2 = \sum_{j=1}^{r} (y_j - \bar{y}_r)^2/r$ for $r = 3,\ldots,n$. Then the $n - 2$ random variables

$$u_{r-2} = G_{r-2}\{(r-2)^{1/2}(y_r-\bar{y}_r)/[(r-1)s_r^2 - (y_r-\bar{y}_r)^2]^{1/2}\} \tag{7}$$

are i.i.d. U(0,1) for $r = 3,\ldots,n$ (O'Reilly and Quesenberry 1973). In applications, one must guard against any systematic arrangement of the data (e.g., ordered from small to large) before applying the transformation given by (7).

Q-Sample univariate (heteroscedastic). Suppose that a random sample $y_{i1},\ldots,y_{i,n_i}$ of size n_i is drawn independently from each of q $N(\mu_i,\sigma_i^2)$ populations ($i=1,\ldots,q$). Then a set of $\sum_{i=1}^{q} (n_i - 2)$ i.i.d. U(0,1) random variables will result by combining the results of applying equation (7) separately to each sample (Quesenberry et al. 1976). The homoscedastic case will be treated by means of an analogous result in terms of the general linear model.

Univariate regression. Suppose that $\underline{y}_n \sim N(X_n\underline{\beta},\sigma^2 I)$ specifies the usual general linear model of full rank under homoscedastic, normality assumptions, where $\underline{\beta}$ is a p x 1 vector of regression coefficients to be estimated. Let $\underline{x}_r'$ denote the r'th row and X_r denote the first r rows of the overall design matrix X_n, $r = p+2,\ldots,n$. Provided that X_r is full column rank, let $c_r = \underline{y}_r'[I - X_r(X_r'X_r)^{-1}X_r']\underline{y}_r$ denote the residual sum of squares after fitting the model $\underline{y}_r = X_r\underline{\beta} + \underline{e}_r$. Then the n - p - 1 random variables $u_{r-p-1} = G_{r-p-1}(v_r)$, where

$$v_r = \frac{(r-p-1)^{1/2}[y_r - \underline{x}_r'(X_r'X_r)^{-1}X_r'\underline{y}_r]}{\{[1-\underline{x}_r'(X_r'X_r)^{-1}\underline{x}_r]c_r - [y_r - \underline{x}_r'(X_r'X_r)^{-1}X_r'\underline{y}_r]^2\}^{1/2}} \qquad (8)$$

are i.i.d. U(0,1) for $r = p + 2,\ldots,n$ (O'Reilly and Quesenberry 1973). In applications, one must avoid any systematic arrangement of the data while at the same time insuring that X_{p+1} is of full rank.

Q-sample univariate (homoscedastic). Suppose that a random sample $y_{i1},\ldots,y_{i,ni}$ of size n_i is drawn independently from each of q, homoscedastic $N(\mu_i,\sigma^2)$ populations ($i = 1,\ldots,q$). Let $n = \sum_{i=1}^{q} n_i$ represent the total sample size. Noting that the linear model $y_{ij} = \mu_i + e_{ij}$ for 1-way ANOVA is full rank, then the previous result applies provided that X_{q+1} contains at least one randomly selected observation from each of the q populations. If $\{y_{r(ij)}\}$ represents a randomized order across all samples of the remaining n-q-1 observations, let $\bar{y}_{(i)}$ represent the sample mean based on $n_{(i)}$ observations from the i'th sample at the r'th step of transformation (8) ($i = 1,\ldots,q$). Let c_r be the corresponding error sum of squares from 1-way ANOVA at the r'th step. Then the n-q-1 random variables

$$u^{(ij)}_{r-q-1} = G_{r-q-1}\{(r-q-1)^{1/2}(y_{r(ij)}-\bar{y}_{(i)})/$$

$$[(1-n^{-1}_{(i)})c_r-(y_{r(ij)}-\bar{y}_{(i)})^2]^{1/2}\} \qquad (9)$$

are i.i.d. U(0,1) for $r = q+2,\ldots,n$. It will usually be informative to reassociate the random variables in their original sample groups once the above transformation has been made. In applications, the most common failure will be to forget to mix all the samples together in some random order before applying transformation (9).

One-sample multivariate. Suppose that $\underline{y}_1,\ldots,\underline{y}_n$ are i.i.d. from a full rank, p-variate $N(\underline{\mu}\ \Sigma)$ population. Let

$$\bar{\underline{y}}_r = r^{-1}\sum_{i=1}^{r}\underline{y}_i, \quad C_r = \sum_{i=1}^{r}\underline{y}_r\underline{y}'_r - r\bar{\underline{y}}_r\bar{\underline{y}}'_r,$$

$$A_r'A_r = C_r^{-1}$$

(a Cholesky decomposition),

$$\underline{z}_r = A_r(\underline{y}_r-\bar{\underline{y}}_r)/[1 - 1/r - (\underline{y}_r-\bar{\underline{y}}_r)'C_r^{-1}(\underline{y}_r-\bar{\underline{y}}_r)]^{1/2}$$

$$= (z_{r1},z_{r2},\ldots,z_{rp})' \ (r=p+2,\ldots,n).$$

Then the p(n-p-1) random variables given by

$$u_{r,s} = G_{r-p+s-2}\{z_{rs}[(r-p+s-2)/$$

$$(1 + z^2_{r1} + \ldots + z^2_{r,s-1})]^{1/2}\} \qquad (10)$$

for $r = p+2,\ldots,n$ and $s = 1,\ldots,p$ are i.i.d. U(0,1) (Rincon-Gallardo et al. 1979).

Clearly, the multivariate, q-sample heteroscedastic case can be treated analogously to the univariate case using (10).

Q-sample multivariate (homoscedastic). Suppose that a random sample $\underline{y}_{i1},\ldots,\underline{y}_{i,n_i}$ of size n_i is drawn independently from each of q, homoscedastic, p-variate $N(\underline{\mu}_i,\Sigma)$ populations ($i = 1,\ldots,q$). Let $n = \sum_{i=1}^{q} n_i$. Proceeding as in the q-sample univariate case, let us select p + q of the observations at random in such a way that at least one observation is selected from each of the q samples, and obtain a randomized order $\{\underline{y}_{r(ij)}\}$ across the samples of the remaining n-p-q observations. Let $\bar{\underline{y}}_{(i)}$ represent the sample mean vector based on $n_{(i)}$ observations at the r'th step of the transformation, and let E_r be the error matrix of SS and SP obtained from 1-way MANOVA at the r'th step. If we obtain the Cholesky decomposition $A_r'A_r = E_r^{-1}$ and define

$$\underline{z}_r = A_r(\underline{y}_{r(ij)}-\bar{\underline{y}}_{(i)})/$$

$$[1-n^{-1}_{(i)}-(\underline{y}_{r(ij)}-\bar{\underline{y}}_{(i)})'E_r^{-1}(\underline{y}_{r(ij)}-\bar{\underline{y}}_{(i)})]^{1/2},$$

$$= (z_{r1},z_{r2},\ldots,z_{rp})' \ ,$$

then by an extension of results given by Rincon-Gallardo et al. (1979), it follows that the p(n-p-q) random variables

$$u^{(ij)}_{r,s} = G_{r-p-q+s-1}\{z_{rs}[(r-p-q+s-1)/$$

$$(1 + z^2_{r1} + \ldots + z^2_{r,s-1})]^{1/2}\} \qquad (11)$$

for $r = p+q+1,\ldots,n$ and $s = 1,\ldots p$ are i.i.d. $U(0,1)$. Again, it will usually be informative to reassociate these random variables in their original sample groups once the transformations are completed.

Assessment of Uniformity

Suppose that $u_{(1)} \leq u_{(2)} \leq \cdots \leq u_{(m)}$ represents the ordered values of m uniform statistics produced by any of the foregoing transformations. Under normality assumptions, the expected value of $u_{(j)}$ is $j/(m+1)$ for $j = 1,\ldots,m$, so that if we plot $u_{(j)}$ vs. $j/(m+1)$ in Cartesian coordinates, then we should expect the points to fall closely about the straight line defined by $g(u) = u$. In q-sample problems, it will generally be informative to assign different symbols to the points associated with the separate samples, or produce separate plots, in making a visual evaluation.

More formally, any of the standard, goodness-of-fit procedures (Pearson's χ^2, Kolmogorov-Smirov one-sample, etc.) can be applied. Miller and Quesenberry (1975) have shown that a modified Watson's U^2 statistic proposed by Stephens (1970)

$$U^2 = (12\ m)^{-1} + \sum_{j=1}^{m} [u_{(j)} - (j - 1/2)/m]^2 - m(\bar{u} - 1/2)^2 , \qquad (12)$$

where $\bar{u} = \sum_{j=1}^{m} u_{(j)}/m$, has attractive power properties as an omnibus test of uniformity. It has the additional advantage of having approximately constant 10, 5, 2.5, and 1 percentage points of 0.152, 0.187, 0.221, and 0.267 respectively for all $m \geq 10$ under the null assumption. The null hypothesis is rejected in this case for large values of U^2. This test in association with transformations given by equations (10) or (11) provides the only known exact test for multi-normality in either the one or q-sample cases. The only apparent disadvantage of these procedures is that the results are somewhat dependent on the order in which the observations are transformed, as we shall see in the following example.

Example. In order to study the effects of data presentation, 24 random permutations of Fisher's iris data, both with and without power transformations were subjected to the q-sample transformation defined by equation (11). The first $p + q = 4 + 3 = 7$ observations for each trial consisted of three randomly chosen versicolor and two each of virginica and setosa.

Table 2. Comparison of U^2 statistics for testing joint normality/homoscedasticity of Fisher's iris data with and without power transformations, using 24 random permutations of the data.

Randomization		Transformation No	 Yes
		(U^2)	(U^2)
1		0.470	0.248
2		0.110	0.084
3		0.243	0.115
4		0.126	0.031
5		0.354	0.130
6		0.364	0.128
7		0.083	0.054
8		0.147	0.105
9		0.603	0.217
10		0.270	0.117
11		0.057	0.060
12		0.260	0.119
13		0.254	0.095
14		0.118	0.115
15		0.199	0.047
16		0.229	0.060
17		0.215	0.059
18		0.218	0.058
19		0.163	0.030
20		0.260	0.174
21		0.354	0.185
22		0.072	0.063
23		0.124	0.069
24		0.251	0.153
	Mean	0.231	0.105
	s.d.	0.130	0.058

$U^2_{0.05} = 0.187$ $\quad U^{2.025}_{0} = 0.221$ $\quad U^2_{0.01} = 0.267$

Table 2 summarizes the U^2 statistics resulting from equation (12) for testing the null hypothesis of joint normality and homoscedasticity. Clearly, VARSTB has had a beneficial impact, as reflected by the reduction of U^2 in every case. Figures 1a -1c show plots of the order statistics from randomization #21 for each variety before transformations were made, while figures 1d - 1f give the analogous results following transformations. It is evident that the setosa values are most affected. Applying the one-sample result of equation (10) to the setosa data alone yielded $U^2 = 0.236$ $(0.01 < P < 0.025)$ before, and $U^2 = 0.208$ $(0.025 < P < 0.05)$ after the transformations. Doubtless U^2 could be reduced still further if VARSTB were applied to the setosa data in isolation from the versicolor and virginica data.

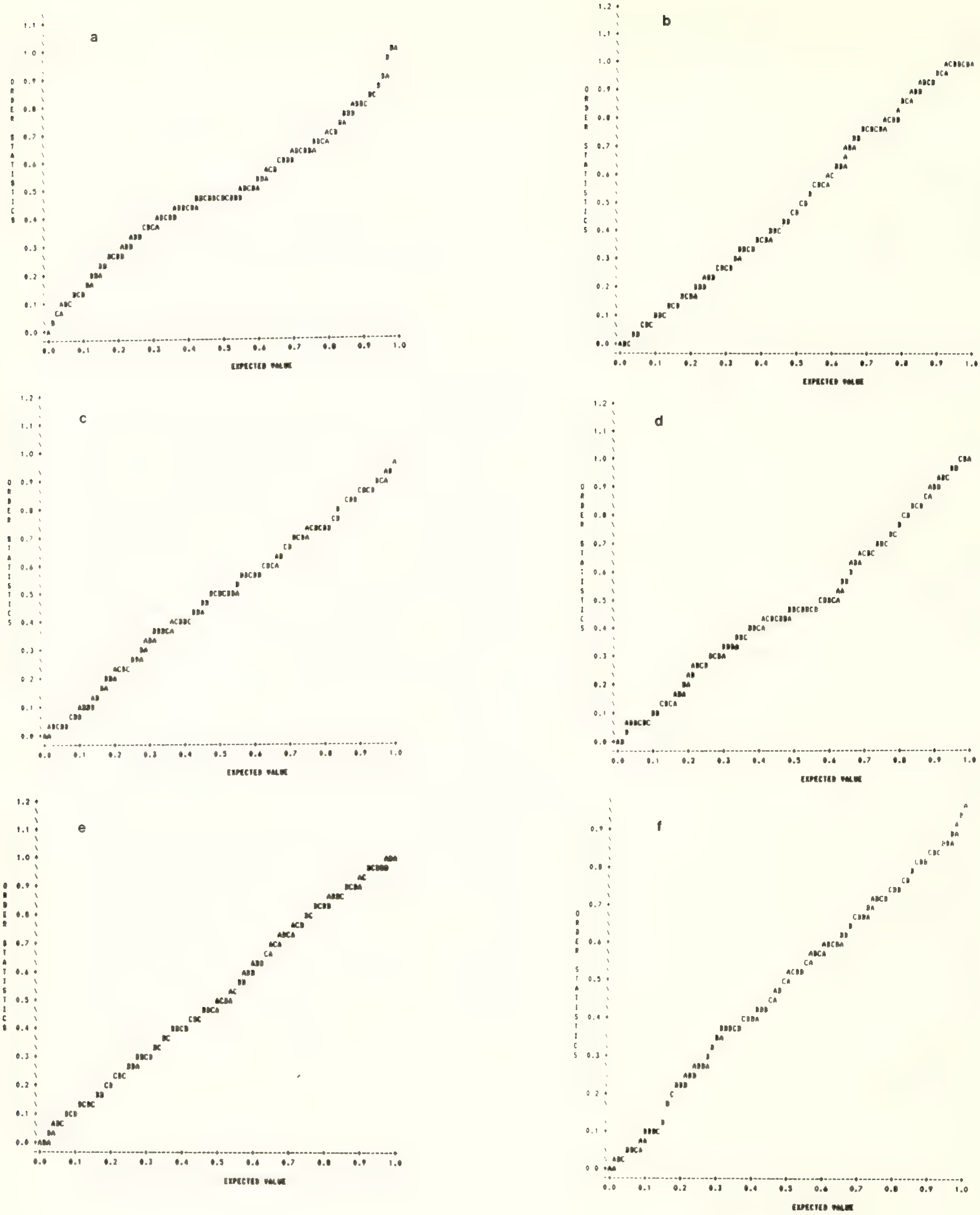

Figure 1. Plot of order statistics for Fisher's iris data: (a) original sertosa (b) original virginica (c) original versicular (d) power transformed sertosa (e) power transformed virginica (f) power transformed versicolor. A = 1 observation, B = 2 observations, C = 3 observations.

Table 3. Observed acceptance rates ($\alpha = 0.05$) for Bonferroni tests of joint normality/homoscedasticity on Fisher's iris data with and without power transformations, based on 24 random permutations of the data.

	Transformation					
	No			Yes		
Summary	Trials/test			Trials/test		
	1	2	5	1	2	5
No. of tests	24	23	20	24	23	20
No. of acceptances	9	5	6	22	22	19
Acceptance rate	0.375	0.217	0.300	0.917	0.957	0.950

A disconcerting finding in table 2 was the extreme variability of U^2 due simply to rearrangements in the order of the data. For the untransformed cases, U^2 was observed to range from a nonsignificant 0.057 to a highly significant 0.603. As summarized in table 3, the null hypothesis acceptance rates ($\alpha = 0.05$) were 0.375 and 0.917 respectively for the original and the transformed data. In order to produce a test of greater overall power in the presence of this lack of symmetry, the logical recommendation is to subject s random permutations of the data to the foregoing procedures. If a signficance level of α/s is used in each trial, and we reject the overall hypothesis if a rejection occurs for any trial, then the familiar Bonferroni result guarantees an overall significance level of at most α. Table 3 summarizes empirical acceptance rates for the Bonferroni procedure with $s = 2$ and $s = 5$ applied to the U^2 statistics of table 2, in the order shown. When $s = 2$, each successive pair was compared to $U^2_{0.05/2} = U^2_{0.025} = 0.221$ for an overall 0.05 level test. The analogous procedure for $s = 5$ employed $U^2_{0.05/5} = U^2_{0.01} = 0.267$. (In actual practice, either exactly $s = 2$ or $s = 5$ permutations would be tested.) Clearly, some increase in power is suggested by the decrease in acceptance rates, particularly when changing from $s = 1$ to $s = 2$ in terms of the untransformed data.

ACKNOWLEDGMENTS

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Applications: Ecological Theory, Habitat Management, Inventory

MULTIVARIATE ANALYSIS OF NICHE, HABITAT, AND ECOTOPE[1]

Andrew B. Carey[2]

Abstract.--Comprehension of the components of a species' response to an environmental complex can be achieved best by partitioning the full range of environmental factors potentially affecting the species (the ecotope hyperspace) into intercommunity factors (the habitat hyperspace) and intracommunity factors (the niche hyperspace). Hyperspaces, and the parts of hyperspaces occupied by a species (hypervolumes), are defined by multidimensional coordinates. Reduction in the number of dimensions of these hyperspaces and hypervolumes to increase comprehension of a species' response to them can be accomplished through multivariate analyses. The analysis of an ecosystem on a south-facing slope of the montane zone in Rocky Mountain National Park, Colorado is presented as an example. Principal component analysis was used to determine the major gradients in a habitat hyperspace defined by 21 environmental variables. Five principal components were interpreted as gradients of soil depth, soil moisture, ground cover, mammal distribution, and shrub abundance. Responses of five species of rodents to these gradients were determined by examining their relative positions on the principal components. Stepwise discriminant analysis (DA) was used to mathematically describe habitat and ecotope hypervolumes of the mammals. Comparison of the major determinants of each hypervolume of each species clarified the niche of the species. Furthermore, the distribution of a major ectoparasite of the mammals was analyzed by DA of environmental variables. Three levels of abundance of the wood tick Dermacentor andersoni could be predicted using only five environmental variables. The presence of a virus infecting both the ticks and mammals could be determined using seven environmental variables.

Key words: Discriminant analysis, ecotope, Eutamias, habitat, niche, principal component analysis, Spermophilus.

INTRODUCTION

Understanding the relationships between a species and its environment is the basic premise for wildlife management; to further this understanding is the foremost goal of wildlife research (Sanderson et al. 1979). Wildlife management and wildlife research have progressed to the point where precise and mathematical definition of basic terminology is necessary for further rapid progress. The response of a species (or ecotype) to its environment is usually examined in one of two contexts: the habitat (its response to extensive features) or the niche (its response to local features). Unfortunately, the communication of research results depends on the assumption of mutual understanding of terminology rather than on a basis of precise definition or an organized system of mathematical descriptions. Haskell (1940) pointed out that this assumption is characteristic of a poorly advanced science.

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Development of multidimensional treatments of habitat and niche (Hutchinson 1958) was concurrent with the adaptation of multivariate statistical methods to ecology (Hughes and Lindley 1955). These methods made practical the application of multidimensional thinking to field studies of species-environment relationships (Cody 1968, Green 1971, Hespenheide 1971, James 1971, Shugart and Patten 1972).

Despite these developments, there is still no unanimity on precise definitions of habitat and niche. Most ecology texts refer to habitat as the "address" and niche as the "profession" of an animal in its environment and later, in a discoursive context, refer to Hutchinson's n-dimensional hypervolume (Odum 1971, 1975; Kendeigh 1974; Smith 1974, 1977; Richardson 1977; Brewer 1979; McNaughton and Wolf 1979). Vandermeer (1972) pointed out that such definitions are excessively vague and inadequate. Whittaker et al. (1973) stated that the two terms, habitat and niche--perhaps the two most important in ecology--are among the most confused in usuage, and that their unsystematic usage has led to further confusion of other terms and concepts.

Nudds (1979) explained the need for applied wildlife research in a theoretical context, and Sanderson et al. (1979) reminded us that one of our major reasons for reporting wildlife research is to transfer that information from the research community to the management community. The need for clarity in interpretation and reports of research results and for some degree of unanimity on terminology is apparent. Whittaker et al. (1973, 1975) proposed a precise terminology (fig. 1) and found support in Hutchinson (1978). Despite objections to this terminology (Kulesza 1975, Rejmanek and Jenik 1975), I believe it offers the precise definition required to maintain a desirable level of clarity in the presentation of species-environment relationships. In this paper I will first discuss the terminology of Whittaker et al. (1973) with some additions from Hutchinson (1978), and then illustrate how it can be applied to a field study of a complex ecosystem. Finally, I will discuss the utility of the terminology in wildlife research and in management.

NICHE, HABITAT, AND ECOTOPE

Landscapes are characterized by spatial gradients of structural (stage-setting or scenopoetic) variables (e.g., elevation, slope, soil fertility), and are composed of biotopes--locations (physical spaces) that have convenient arbitrary upper and lower boundaries, and that are horizontally homogeneously diverse (their structural elements are small compared with the range of an individual) relative to the larger motile organisms within them. These biotopes in the landscape pattern contain recognizable communities (fig. 1). Biological communities, however defined, are vaguely bound in space and time (Inger and Colwell 1977). The biotic context of a population is its community--an association of coexisting populations bound functionally by their interactions and spatially by their co-occurrence in a biotope (Colwell and Fuentes 1975).

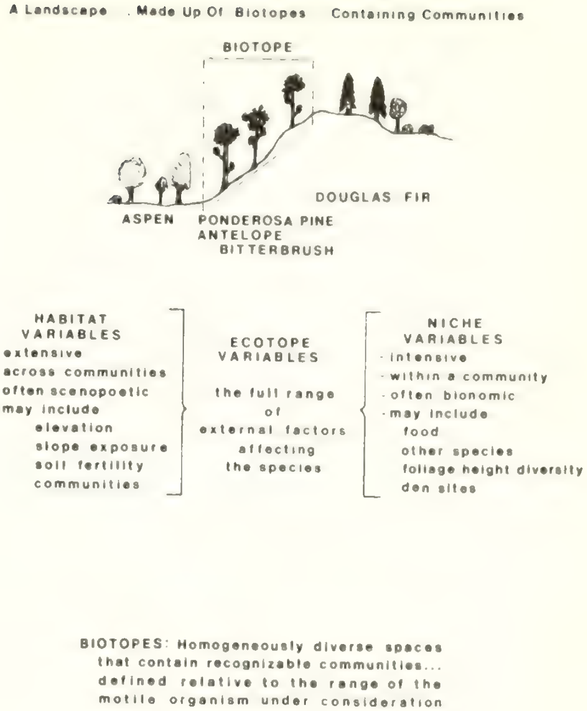

Figure 1. A suggested terminology.

The environmental variables with extensive spatial components are intercommunity or habitat variables; axes derived from these variables describe a multidimensional habitat hyperspace. Each species in the landscape occurs over some range of the habitat variables; the limits of these ranges define a habitat hypervolume--a fraction of the habitat hyperspace where a species occurs. Multivariate analyses can be used to reduce the number of dimensions defining hyperspaces and hypervolumes, and this allows comparison of the habitat relationships of the many species populations found in the habitat hyperspace. The response of a species population to habitat variables within its hypervolume describes its habitat; Maguire (1973) provided a method for examining such responses in terms of isopleths of population parameters projected on axes representing the reduced dimensions.

The intracommunity or niche variables (intensive or local environmental variables, e.g., height above ground, seasonal time, prey size, "microhabitat" variables) likewise define a niche *hyperspace* that interrelates the species of a community. The niche hyperspace is analagous to the fundamental or preinteractive Hutchinsonian niche. Each species in the community differentially utilizes, occurs in, or is affected by some range of these variables; limits of these ranges define the *niche hypervolume*—a fraction of the niche hyperspace where the species occurs. The niche hypervolume is analagous to the realized or postinteractive Hutchinsonian niche including the "included niche" of Miller (1964). Niche variables are generally bionomic variables (resources for which there may be competition) and may define axes representing other member species of the community. The dimensions of niche hyperspaces and hypervolumes can be reduced through multivariate analyses, and isopleths of the population response to the niche variables (the *niche*) can be projected on them (Maguire 1973).

The landscape of communities (the compound hyperspace that represents the full range of external circumstances to which species in the landscape are adapted) is the *ecotope hyperspace* and contains an *ecotope hypervolume* defined by a species' limits on the ranges of the ecotope variables. The *ecotope* represents the full range of a species' adaptation to external factors and is the ultimate arena for consideration of its relations to its environment (especially in a broad evolutionary context), whereas the niche focuses on the role of the species within its community (especially competitive interactions), and the habitat relates to the distributional response of the species to the intercommunity environmental factors (those with extensive spatial components). Niche differences are intracommunity differences and involve genetic characteristics evolved in relation to other species; habitat differences reflect the evolutionary response to a gradient of environmental factors external to, although often modified by, the community. Niche breadth measures intrapopulation genetic characteristics; habitat breadth measures interpopulation differentiation based on mechanisms different from those responsible for niche breadth, for example, ecotypic and subspecific differentiation.

It can be seen readily that most wildlife management efforts do deal with habitat variables; however, the strength of the concepts is that they provide a conceptual scheme for different kinds of diversity (Hutchinson 1978) and, with increased interest in managing diversity (Pimlott 1969, Siderits and Radtke 1977), the wildlife biologist may want to deal with niche differences (within habitat or alpha-diversity), habitat differences (between habitats or beta-diversity), or with broad geographical differences (gamma-diversity).

The basic principle underlying multivariate analyses of species-environment relationships is the determination of points (limits of ranges of niche, habitat, or ecotope variables) in multidimensional space followed by the mathematical reduction of the number of dimensions so that those remaining are all orthogonal, independent, and significant (Hutchinson 1978).

AN ILLUSTRATION: A MONTANE ECOSYSTEM

The landscape chosen for study (Carey et al. 1980) included two south-facing slopes of the upper montane forest climax region in the Rocky Mountain National Park, near Estes Park, Colorado. The areas encompassed about 20 ha of varied terrain, ranging from steep (>30°) slopes with massive rock outcrops to gentle (2-8°) slopes with deep soil. Elevation was between 2,487 and 2,585 m, and the areas were representative of the upper montane, and contained all major plant communities found there: aspen stand complex, ponderosa pine complex, big sagebrush complex, and dry montane grassland complex (Marr 1967). Five species of rodents were abundant on the areas; in order of decreasing abundance they were deer mice (*Peromyscus maniculatus*), Richardson's ground squirrels (*Spermophilus richardsonii*), golden-mantled squirrels (*S. lateralis*), least chipmunks (*Eutamias minimus*), and Uinta chipmunks (*E. umbrinus*).

Methods

Sampling grids were surveyed on the two areas and consisted of 269 intersections (marked by stakes) 30 m apart (13x13 stakes on one area, 10x10 stakes on the other). A number of structural variables (table 1) were measured on the 225 30m x 30m quadrats covering the 20 ha. Seven plant-frequency counts were taken from 20cm x 20cm quadrats randomly placed in the vicinity of each stake. Four traps (for small mammals) were placed in the vicinity of each stake; these were operated for 46,000 trap nights. Fecal samples were collected from droppings beneath traps containing a chipmunk or ground squirrel. Fecal samples were analyzed by the microhistological method (Sparks and Malechek 1968) to obtain the dietaries of the species populations. Blood samples for Colorado tick fever virus isolation attempts were collected from a subsample of the captured rodents. Traps for adult, free-ranging ticks were placed in the center of 128 of the 225 quadrats and were operated for 1,200 trap nights. For detailed procedures see Carey et al. (1980).

Statistical Analyses

Structural variables that were highly correlated (>0.90) with simpler (not transgenerated or more easily measured) variables or that were invariant (e.g., DIRNSL) were deleted from the data set. The remaining variables were averaged over the sets of four contiguous quadrats surrounding each point location (stake) in the landscape. These variables were taken to represent habitat variables, and mean values for each point location were paired with values of the rodent-capture variables for that point location (total captures of the five most abundant

Table 1. Structural variables measured on 30m x 30m quadrats or transgenerated from measured variables.

Acronym	Structural variable
SOILD:	mean depth of soil exclusive of areas with < 5 cm of soil
%SOIL2:	percent of quadrat with soil < 5 cm in depth
%EXPRK:	percent of quadrat covered by exposed rock
RKRK:	rank (0-4)[1] of exposed rock for interstices
DSLOPE:	degree of slope
DIRNSL:	aspect (compass degrees)
GRASSL:	ranked abundance (0-4) of grass litter
PINEL:	ranked abundance (0-4) of pine needles and cones
WDDEBR:	ranked abundance (0-4) of wood debris less than 15 cm in diameter
LNFTLG:	length of logs > 15 cm diameter multiplied by diameter
DECOMP:	rank (0-4) of decomposition of log litter
SMPINE:	number of coniferous trees < 15 cm dbh
LGPINE:	number of coniferous trees > 15 cm dbh
NASPEN:	number of quaking aspen
%SHRUB:	percent of quadrat covered by shrubs
PUTR-P:	presence-absence (1,0) of antelope bitterbrush
RICE-P:	presence-absence (1,0) of wax currant
ARTR-P:	presence-absence (1,0) of basin big sagebrush
NJUSC:	number of Rocky Mountain junipers
DJUCO:	diameter (cm) of common junipers
ARLU-RK:	ranked abundance (0-4) of Louisiana sagewort
ARFR-RK:	ranked abundance (0-4) of fringed sagewort
ROAC-RK:	ranked abundance (0-4) of prickly rose
OPPO-RK:	ranked abundance (0-4) of plains pricklypear
PESI-RK:	ranked abundance (0-4) of mountain ball cactus
CHVI-P:	presence-absence (1,0) of Douglas rabbitbrush
EXPRKRK:	%EXPRK x RKRK
SHPUTR:	%SHRUB x PUTR-P
SHRICE:	%SHRUB x RICE-P
SHARTR:	%SHRUB x ARTR-P
SLPEXR:	DSLOPE x %EXPRK
TOPINE:	SMPINE + LGPINE
LNFTDC:	LNFTLG x DECOMP

[1] Rank (0-4): Absent, 0; sparse, 1; scattered, 2; common, 3; abundant, 4.

species). Principal component analysis (PCA) (Dixon 1976) was used to generate a smaller number of new variables (to reduce dimensions of the data set) that were interpreted as spatial gradients or major axes of the habitat hyperspace. Mammal-capture variables were included in the analysis to obtain a measure of the habitat, or response, of each species to the hyperspace gradients.

Point locations were grouped into species' ecotope and habitat hypervolumes and remaining hyperspaces according to the presence of each rodent species except for Richardson's ground squirrels and deer mice. The criterion for grouping stations in terms of Richardson's ground squirrels was that two or more ground squirrels had been captured near the point location. This criterion was used because single captures were scattered, and multiple-capture locations were clumped in distribution. The scattered captures presumably resulted from breeding season movements and dispersal behavior (Hansen 1962, Yeaton 1972, Michener and Michener 1977) and therefore, did not reflect habitat. Deer mice were trapped at virtually all locations.

The habitat hypervolumes of chipmunks and ground squirrels were mathematically described by stepwise discriminant analysis (DA) (Dixon 1976) of 21 of the habitat (scenopoetic) variables. The ecotope hypervolumes of the sciurids were similarly described by stepwise discriminant analysis of 9 habitat variables, 11 plant-frequency variables representing the distribution of the major food items of sciurids, and 4 mammal-capture variables (the four abundant species of rodents other than the species under consideration); these 24 variables collectively constitute ecotope variables. Results of the stepwise procedures (the best discriminating variables are chosen first) for the habitat and ecotope hypervolumes of a single species were compared to determine if the species was responding to habitat (scenopoetic) variables or to niche (bionomic) variables.

Distributions of adult ticks and virus in the landscape were described mathematically by discriminant analysis of structural variables (Carey 1979). The purpose of this analysis was to determine if enough information was contained in the structural variables to allow DA to generate discriminant functions (DF) that would be useful in classifying other parts of the landscape into categories of relative abundance of ticks and virus. A jackknife procedure (Brown 1977) was used to obtain less biased estimates of the error of classification of these discriminant functions.

Results

Principal Component Analysis

Five principal components (PC) were interpreted (table 2). These accounted for 64% of total variance in the data.

PC1 is a soil depth gradient in the habitat hyperspace. Measures of shallow soil, exposed rock, and slope were heavily weighted at one end with deep soil measures at the other end. CHVI-P, ROAC-RK, and SRICH were at the deep soil end. Douglas rabbitbrush (Chrysothamnus viscidiflorus) was most abundant in areas of deep dry soil, and prickly rose (Rosa acicularis) was most abundant in areas of deep moist soil. Richardson's ground squirrels were abundant in areas of deep soil.

PC2 is a soil moisture gradient. Quaking aspen (Populus tremuloides), lush grass, and prickly rose were found on moist soil. Big sagebrush (Artemisia tridentata) grew only on deep dry soil, as did Douglas rabbitbrush. Fringed sagewort (Artemisia frigida) and shrub cover (antelope bitterbrush, Purshia tridentata, etc.) were well distributed over areas with dry soil.

PC3 is ground cover and abundant vegetation measures oppose litter measures. The order is vertical vegetative diversity, ranging from trees to shrubs to litter. PINEL was not highly correlated with TOPINE (r=0.16); pine litter accumulated in relatively closed stands and around scattered over-mature trees.

PC4 is mammal distribution in the habitat hyperspace. Richardson's ground squirrels (SRICH)are at one extreme of the component and the golden-mantled squirrels (SLAT) and chipmunks (TOTCH) are at the other extreme; the deer mice (PMAN) are in the middle.

PC5 is a shrub abundance variable. Shrub measures are at one end and exposed rock measures are at the other end. The presence of CHVI-P seems to contradict the interpretation of PC5. However, CHVI-P was a presence-absence variable, not a measure of abundance. Douglas rabbitbrush was found in the absence of other shrubs in some deep dry soils and the stands of big sagebrush and antelope bitterbrush in other areas; it was rarely found in stands where antelope bitterbrush grew together with wax current (Ribes cereum) and boulder raspberry (Rubus deliciosus). TOPINE is associated with low shrub abundance in PC5; shrub cover was very low in pine stands.

Table 2. The principal components and their variable coefficients (from Carey et. al. 1980).

PC1--Soil depth		PC2--Soil moisture		PC3--Ground cover		PC4--Mammal distribution		PC5--Shrub abundance	
Variable	Coeff.	Variable	Coeff.	Variable	Coeff.	Variable	Coeff.	Variable	Coeff.
%SOIL2	0.36	NASPEN	-0.35	PINEL	-0.36	SLAT	0.37	SHARTR	-0.39
%EXPRK	0.31	ROAC-RK	-0.29	WDDEBR	-0.27	TOTCH	0.34	%SHRUB	-0.37
TOPINE	0.28	GRASSL	-0.24	LNFTLG	-0.23	WDDEBR	0.29	ARLU-RK	-0.36
EXPRKRK	0.26	NJUSC	-0.23	SLAT	-0.13	EXPRKRK	0.23	DJUCO	-0.31
ARLU-RK	0.26	SOILD	-0.22	CHVI-P	-0.07	%SHRUB	0.23	LNFTLG	-0.29
DSLOPE	0.24	DJUCO	-0.17	%SOIL2	-0.07	SHARTR	0.21	NJUSC	-0.21
NJUSC	0.23	PINEL	-0.15	DJUCO	-0.01	SOILD	0.17	ROAC-RK	-0.14
PMAN	0.17	TOTCH	-0.08	ARLU-RK	0.03	%EXPRK	0.17	WDDEBR	-0.15
LNFTLG	0.15	SRICH	-0.06	NJUSC	0.04	DJUCO	0.17	NASPEN	-0.09
SLAT	0.15	LNFTLG	-0.05	SOILD	0.08	CHVI-P	0.15	ARFR-RK	-0.09
WDDEBR	0.11	WDDEBR	-0.00	ARFR-RK	0.11	NASPEN	0.12	%SOIL2	-0.06
TOTCH	0.07	%SOIL2	0.00	%SHRUB	0.15	ROAC-RK	0.11	GRASSL	-0.05
ARFR-RK	0.04	%EXPPRK	0.01	SHARTR	0.16	PINEL	0.10	DSLOPE	0.00
PINEL	0.02	ARLU-RK	0.01	%EXPRK	0.19	PMAN	0.06	TOTCH	0.02
DJUCO	-0.05	PMAN	0.03	SRICH	0.18	LNFTLG	0.02	SRICH	0.05
SHARTR	-0.09	SLAT	0.05	TOTCH	0.19	GRASSL	0.02	SOILD	0.07
NASPEN	-0.10	EXPRKRK	0.07	EXPRKRK	0.20	TOPINE	0.02	PMAN	0.09
%SHRUB	-0.12	TOPINE	0.09	PMAN	0.22	NJUSC	0.01	PINEL	0.13
GRASSL	-0.14	DSLOPE	0.15	GRASSL	0.27	%SOIL2	-0.03	TOPINE	0.15
ROAC-RK	-0.17	CHVI-P	0.26	NASPEN	0.28	DSLOPE	-0.10	%EXPRK	0.19
SRICH	-0.22	ARFR-RK	0.33	DSLOPE	0.30	ARLU-RK	-0.16	SLAT	0.20
CHVI-P	-0.28	SHARTR	0.34	TOPINE	0.31	ARFR-RK	-0.35	CHVI-P	0.21
SOILD	-0.28	%SHRUB	0.34	ROAC-RK	0.32	SRICH	-0.35	EXPRKRK	0.27
Eigenvalue	6.3		3.6		2.2		2.1		1.7
Cumulative percent[1]	0.25		0.40		0.49		0.57		0.64

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[1] Cumulative proportion of total variance explained by the principal components.

Thus, the major gradients in the habitat hyperspace were soil depth and soil moisture, and they accounted for two-thirds of the explained variance. Smaller portions of the variance were explained by ground cover, mammal distribution, and shrub abundance. Barkham and Norris (1970) pointed out that it is not uncommon for minor components to increase in complexity and to represent interaction effects. The last three components probably do, in part, represent the interaction of soil depth and soil moisture. PCA illustrated the plants' and mammals' responses (habitats) to the habitat hyperspace. Richardson's ground squirrels were strongly associated with deep soils (PC1). Golden-mantled ground squirrels were moderately associated with shallow soils (PC1) and exposed rock (PC1, PC5). Chipmunks were associated with golden-mantled squirrels (PC4). Deer mice were associated with grasses (PC3) and were intermediate on the other PC's. All of the mammals occupied intermediate positions on the soil moisture gradient. This indicates that soil moisture was not a major determinant of any species' habitat hypervolume and suggests that mammal distributions were a function of soil depth. Richardson's ground squirrels almost exclusively used ground burrows for escape and denning. They assumed a characteristic "picket pin" posture for observation. They did not use rocks for escape or observation in the study areas. Golden-mantled ground squirrels used large rocks as observation, feeding, and basking posts. They commonly used rock interstices for escape cover and den sites. Chipmunks also used rocks as observation posts, escape cover, and den sites.

Discriminant Analyses on Mammals

Results of DA on data sets of the habitat and ecotope hyperspaces are illustrated in table 3. The first five steps and the last step of the DA are shown. Group means of the habitat hypervolume and the remaining hyperspace were significantly different (P<0.001) at each step for all species except the least chipmunk. For the least chipmunk, P=0.012 at the first step and P=0.019 at the last step. Group means of the ecotope hypervolume and the remaining hyperspace were significantly different (P<0.001) at each step for all species. Rates of change in the U statistics and the percentages of stations correctly classified showed that most information contained in the DF's was contributed by the first few variables in each case. More stations were classified correctly with the ecotope hyperspace variables than with the habitat hyperspace variables. U statistics were lower and station classifications were more successful for golden-mantled ground squirrels and Richardson's ground squirrels than for Uinta chipmunks and least chipmunks.

Comparison of discriminating variables between the habitat hypervolumes and the ecotope hypervolumes showed that the ecotope hypervolume of the Richardson's ground squirrel differed little from its habitat hypervolume, and that its distribution was a response primarily to a structural variable, soil depth, and incidentally to a bionomic variable, captures of golden-mantled ground squirrels. The golden-mantled ground squirrel's distribution was a function of bionomic variables--captures of other mammals (primarily Richardson's ground squirrels)--rather than a response to habitat (structural) variables. Habitat variables (e.g., EXPRKRK) were equal in importance to bionomic variables (e.g., captures of golden-mantled ground squirrels) in describing the distribution of least chipmunks. The Uinta chipmunk responded to habitat variables.

Table 3. Results of stepwise discriminant analysis of hyperspaces for Spermophilus lateralis (modified from Carey et al. 1980).

Variable set	Step[1]		U	%
Habitat	1	%SOIL2	0.87	66
	2	WDDEBR	0.81	72
	3	CHVI	0.79	75
	4	PINEL	0.78	75
	5	EXPRKRK	0.77	76
	21	GRASSL	0.72	77
Ecotope	1	SRICH	0.67	86
	2	PMAN	0.65	86
	3	ARLU-F	0.64	87
	4	EMIN	0.63	87
	5	%SHRUB	0.62	86
	24	EXPRKRK	0.59	88

[1] Step in stepwise procedure, variables included, Wilks λ, cumulative percent of stations properly assigned. All group means signifincantly different at all steps (P<0.01).

Summary of Species-Environment Relationships

Richardson's Ground Squirrel.--Food habits of the Richardson's ground squirrels were similar to those of the golden-mantled ground squirrels. Spatial overlap between the two species in the habitat hyperspace was moderate, and ratios of the mean captures of the two in each other's habitat hypervolume were inversely related. Diet overlap with the least chipmunk was small; spatial overlap moderate. Richardson's ground squirrels were at one end of the mammal distribution component, and golden-mantled ground squirrels and chipmunks at the other end. PCA and means of the discriminating variables showed that the habitat hypervolume of Richardson's ground squirrel was characterized by deep soil, vegetative ground cover, and slight slopes. It was not characterized by either extreme of soil moisture, or by high values of exposed rock or shrub cover. Discriminating variables for the ecotope hypervolume demonstrated the overwhelming influence of the habitat (structural) variables, especially soil depth measures, but also indicate a degree of negative response to the golden-mantled ground squirrels.

Golden-mantled Ground Squirrels.--Trophic overlap was great with Richardson's ground squirrel, and moderately low with the least chipmunk. Spatial overlap was small with Richardson's ground squirrel, and great with the least chipmunk. Capture ratios were inversely related with the ground squirrel, and one-sided with the chipmunk (in favor of the golden-mantled ground squirrel). Their habitat hypervolume was characterized by shallow, somewhat dry soil on steep slopes with sparse grass cover, moderate tree (ponderosa pine, *Pinus ponderosa*) cover, abundant litter, and abundant exposed rocks with interstices. The best discriminating variable for the ecotope hypervolume was the captures of Richardson's ground squirrel, a bionomic variable. Other discriminating variables contributed little to the description of the ecotope hypervolume.

Least Chipmunk.--Overlap between the diet of least chipmunks and those of ground squirrels was small; the least chipmunk made greater use of arthropods for food than did ground squirrels. Spatial overlap with the golden-mantled ground squirrel was high. The ground squirrel was near 92% of the point locations in the chipmunk habitat hypervolume and outnumbered chipmunks throughout the habitat hyperspace. The habitat hypervolume of the least chipmunk was characterized by intermediate soil depth and moisture, moderate vegetative ground cover, and higher than average values of exposed rock, rock interstices, prickly rose, aspen, pine trees (*P. ponderosa* and *P. contorta*), and common juniper (*Juniperus communis*). Exposed rock with numerous interstices was the single best descriptor of the habitat hypervolume, regardless of whether rocks were in conjunction with deep or shallow soils, pine trees or aspens, or shrubs or grass. The ecotope hypervolume was characterized by the presence of golden-mantled ground squirrels. Deep soil indicators (NASPEN, POPR-F, ARTR-F) were less important discriminating variables, and described the part of the hypervolume not characterized by golden-mantled ground squirrels, for example, small rock outcrops in deep soil areas.

Uinta Chipmunk.--Uinta chipmunks were relatively few in number and were caught in only 16% of the trap stations. Their habitat and ecotope hypervolumes were characterized by the highest mean values for shallow soil, exposed rock, rock interstices, steep slopes, log litter, and pine trees, and by the lowest mean values for soil depth, shrub cover, grass litter, and deep soil indicators, such as prickly rose and Douglas rabbitbrush.

Discriminant Analyses on Ticks and Virus

Ticks.--The relationship between habitat variables and adult wood tick abundance is illustrated in table 4. High tick abundance was associated with shallow soil, moderate shrub cover, abundant exposed rock and rock interstices, steep slopes, relatively abundant pine, and abundant log litter. Moderate tick abundance was associated with intermediate values of the same variables, except for shrub cover, which was abundant. The distribution of ticks in the habitat hyperspace reflects their physiological tolerance for soil temperatures and moisture (Wilkinson 1967).

The objectives of the DA of tick distribution were to obtain DF's of variables that were easily and quickly measured and that provided a high degree of discriminance in classifying areas on the basis of tick abundance. The discriminant functions in table 4 met those objectives. The two best discriminating variables were DSLOPE and %SOIL2. Less biased estimates of errors of misclassification were obtained with jackknifing procedures; they differed little from the cumulative percentages in table 4 (Carey 1979).

CTF Virus.--The relationship between virus activity and the ecotope hyperspace variables was illustrated by Carey (1979). Virus was isolated from mammals captured in areas characterized by shallow soil, abundant exposed rocks and rock interstices, relatively abundant pine, moderate shrub cover, moderately steep slopes, relatively high numbers of golden-mantled squirrels, least chipmunks, Uinta chipmunks, deer mice, and immature ticks, and low numbers of Richardson's ground squirrels. The objective of the DA of virus distribution was to obtain DF of easily measured variables that would permit identification of areas maintaining virus circulation with a low probability of misclassifying areas with virus. The DF met this objective (Carey 1979).

DISCUSSION

I believe the foregoing is a demonstration of precise definition combined with methods of multivariate analysis. After the terminology is grasped, the results should be ordered and clear to the reader. The distinction between structural (scenopoetic) variables and bionomic (potentially measuring competition) variables should be clear; also the differences in scope between habitat (intercommunity), niche (intracommunity), and ecotope variables should be clear. The enforced distinction between niche, habitat, and ecotope results in heuristic data analysis and interpretation of results that is clear. The compatibility between the terminology and the analysis is obvious.

Table 4. Discriminating variables and discriminant functions for the distribution of adult, free-ranging wood ticks. All group means significantly different at P<0.01 using approximate F tests.

Variable	U	Cumulative[1] %	DF Coefficients[2] None-Few ticks	DF Coefficients[2] Few-Many ticks
%SOIL2	0.519	62.5	0.21450	0.25643
DSLOPE	0.360	68.8	0.19518	0.44237
%SHRUB	0.324	72.7	0.24368	0.21132
ARLU-RK	0.302	72.7	1.16317	2.19884
SOILD	0.291	73.4	1.23637	1.21552
GRASSL	0.281	74.2	-0.17259	-0.78330
NASPEN	0.263	76.6	0.33857	2.63709
Constant			-14.55902	-21.57874

[1] Cumulative percentages of stations correctly assigned by the DF.

[2] Coefficients of the variables for the discriminant function separating the two groups.

These concepts (the ecological and the statistical) have been used to good advantage in the past, but, I believe, without precise definition. James (1971) clearly distinguished between intercommunity and intracommunity relationships in addition to formulating the niche-gestalt. Anderson and Shugart (1974) used the same (Whittaker et al. 1973) definition of habitat hyperspace. Dueser and Shugart (1978, 1979) also recognized the distinction between inter- and intracommunity relationships, but used a plethora of terms (habitat, microhabitat, habitat type, habitat association, habitat patch, patch type, forest stand type, forest type, desert community, rodent community, forest biome, fine-grained environment, etc.) in the 1978 paper (I am not criticizing the quality of their scientific contribution, I am pointing out the lack of precise terminology). Similarly M'Closkey (1975, M'Closkey and Fieldwick 1975) recognized the inter- and intracommunity distinction and the applicability of multivariate analysis (M'Closkey 1976) to the study of animal-environment relationships but not the use of precise terminology.

The use of the suggested terminology and multivariate analysis in the study of animal-environment relationships is clear, but what about the applicability to wildlife management? Aside from the basic understanding of how a species (or ecotope) responds to its environment, I think the inter- and intracommunity distinction is one that will prove to be of great value to the wildlife biologist, especially if the trend towards management for diversity continues. The distinction between structural and bionomic variables is useful at the management level; extensive management must focus on scenopoetic variables, but intensive management can consider bionomic variables. Understanding the concepts of spatial gradients and species' responses to them is fundamental to predicting results (or "environmental impact") of a management decision. The concept of homogeneously diverse biotopes coupled with inter- and intracommunity distinctions is of great value in determining scale or size for both sampling units and managing units.

The use of the terms "hyperspace" and "hypervolume" may be confusing and, therefore, of less benefit. Simpler terms, for example "preinteractive" (or fundamental) and "postinteractive" (or realized) could be used to modify "niche space" and "habitat space" without changing the concepts. Applying theoretical concepts to field studies can be rewarding. In the example given, discriminant functions for the ticks and virus could be used to locate recreational facilities and activities for minimum human exposure to the virus. The tick discriminant function could be used in the application of acaricides. Richardson's ground squirrel is a reservoir of plague (Yersinia pestis), and the golden-mantled ground squirrel is a reservoir of Colorado tick fever virus. Results of the analysis suggest that if Richardson's ground squirrels were controlled (killed) to minimize human exposure to plague (such a control effort was instituted in 1976 and 1977), they would be replaced by golden-mantled ground squirrels. This would not increase the risk of human exposure to Colorado tick virus, because the golden-mantled ground squirrels would have moved out of the area that was climatically suited for ticks.

Many authors, especially Green, (1971, 1974) have discussed the applicability of multivariate analyses in ecology; most of the comments apply equally to wildlife research. However, I have seen only two reports in the Journal of Wildlife Management (Klebenow 1969, Martinka 1972) describing the application of multivariate analyses to animal-environment relationships. I believe a functional organization and a standardization of ecological terminology can do much to promote the application of multivariate statistics to the more applied areas of wildlife reasearch.

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DISCUSSION

BOB CLARK: Were there age and sex biases in the captures?

A.B. CAREY: Possibly. I attempted to minimize biases due to age and sex by disregarding single captures of Richardson's ground squirrels, to trap-happiness by only using the first capture of an individual in a sampling period, and to competition for traps by placing four traps at each point location in the landscape and by checking the traps up to four times daily.

BOB CLARK: By removing biases due to dispersal, would you improve the discrimination of the habitats?

A.B. CAREY: Yes. However, the sample size was large and dispersal movements probably accounted for a small proportion of the captures used as captures seemed to be very clumped. In regards to other biases, it should be emphasized that I was interested only in generating a relatively crude measure of population response with the objective of determining hypervolumes.

KEN MORRISON: Given that there are behavioral biases inherent in trapping data, would this bias any results and/or interpretations of such an analysis?

A.B. CAREY: Yes, but see previous response to Bob Clark.

R. DUESER: How important is the notion of the "homogeneously diverse biotope" to your distinction between "niche" and "habitat"? What would be the implications of the non-existence of homogeneously diverse biotopes?

A.B. CAREY: The distinction between niche and habitat is that between intra- and inter-community, thus one must be able to assign a point location in the landscape to a recognizable community which occupies the homogeneously diverse space called the biotope, thus the notion is fundamental. "Homogeneously diverse" is relative to the range of a motile organism; if communities exists, so do biotopes; if they do not, niches don't either.

JAMES DUNN: (1) If the principal components are properly named, can variation in soil really be independent of moisture? (2) Can variation in mammal distribution really be independent of variation in ground cover? (3) Why not confess that the fundamental variables need not be independent and proceed with an oblique factor solution. The additional benefit might be a measure of the association between say mammal factor and cover factor if essentially the same named factors result?

A.B. CAREY: (1) Soil depth and soil moisture can be quite independent as is reflected by the community pattern in the landscape e.g., basin-big sagebrush on deep dry soils, and aspen stand complexes on deep wet soils. (2) Variation in mammal distribution can be independent of "ground cover" especially in a homogeneously diverse space. (3) Principal components beyond the 1st and 2nd components may show interaction effects (Barkham & Norris 1970) as mine do. However, I think my principal components nicely describe the spatial gradients in the landscape. I would say den sites (ground dens, rock dens) were more important than vegetative cover; there is also good evidence that food is not limiting and that the behavior of the species causes them to avoid the densest cover.

FORHAB: A FOREST SIMULATION MODEL TO PREDICT HABITAT STRUCTURE FOR NONGAME BIRD SPECIES[1]

T.M. Smith[2], H.H. Shugart[3], and D.C. West[4]

Abstract.--FORHAB (a deciduous forest stand stimulation model) was used to predict changes in available breeding habitat for the avian community inhabiting the Walker Branch Watershed in east Tennessee. A census was conducted to locate all breeding territories of the various bird species on the watershed. Data on vegetational structure of these territories were used to calculate linear decision scales, a classification procedure based on discriminant function analysis, which could be used to classify forest stands as potential breeding habitat for the various bird species. FORHAB was used to simulate changes in forest structure of the watershed due to both natural succession and certain introduced forest management practices (diameter-limit cut). Variables describing the vegetational structure of the forest stands generated by FORHAB were used to determine availability of potential breeding habitat for each bird species through time using a subroutine based on the above-mentioned classification procedure. Predictions of available habitat for the ovenbird (Seiurus aurocapillus) on the Walker Branch Watershed are presented as an example of model output.

Key words: Avian community; deciduous forest; discriminant function analysis; forest management; linear decision scales; nongame birds; simulation model; vegetation structure.

INTRODUCTION

The effects of modern forest management practices on wildlife has been a subject of growing concern in recent years (Slusher and Hinckley 1974, Thomas 1979). A major portion of this interest has been directed toward the nongame bird component of an animal community (Smith 1975, DeGraaf 1978) particularly the effect that management-related disturbances have on the population dynamics of either a single species (e.g., endangered species) or the avian community as a whole. The majority of work in this area has been of a descriptive nature. Researchers have dealt primarily with general habitat preferences of selected species (fig. 1) or the role of structural heterogenity on the overall avian diversity of the forest (MacArthur and MacArthur

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1961). This information, coupled with a knowledge of effects of various silvicultural practices on structure of the forest, has been the basis of timber-wildlife management decisions to date. Problems of time and expense have limited the number of actual field studies which have monitored directly the effects of timber management on bird populations (Hagar 1960, Franzreb and Ohmart 1978). However, even these studies are of limited value. Site-specific conditions and past history of the forest greatly limit the generalization of results from a specific study to other forests.

Recently, techniques of multivariate statistics have allowed analyses beyond qualitative methods of describing habitat preferences of avian species. With the use of multivariate statistical procedures, one can classify forest stands quantitatively with respect to habitat potential. Multivariate data analysis has been used to quantify the microhabitat selection patterns at both the species and community level (James 1971, Shugart and Patten 1972, Anderson and Shugart 1974, Whitmore 1975). Conner and Adkisson (1976) proposed a method of classifying forest stands as suitable woodpecker habitat using a discriminant function analysis procedure based on variables describing structure of forest vegetation and stressed the potential of such techniques as management tools. However, applicability of such statistical procedures is hindered by lack of habitat data necessary for dynamic habitat analyses. Management is by definition a dynamic process. To assess potential effects of various management strategies on availability of habitat, quantitative data describing changes in structure of the forest through time is necessary. To date, quantitative information on structural changes of the forest resulting from various timber management practices is not available. A forest stand simulation model may very well remedy problems inherent in assessing habitat modifications associated with various management techniques.

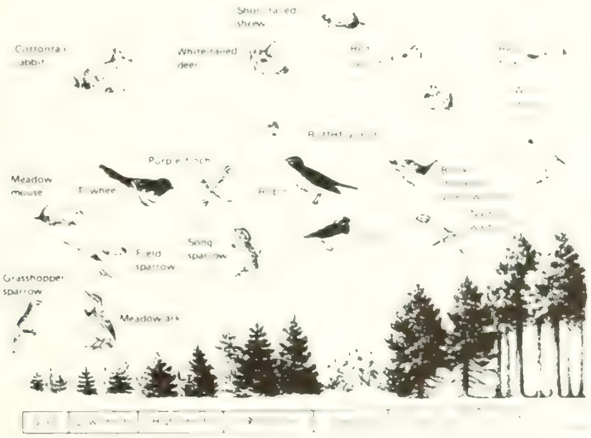

Figure 1. General habitat preference of various animal species inhabiting a northeastern conifer forest. [Reprinted with permission from Smith (1980)].

Forest stand simulators (Shugart and West 1980), can be used to assess effects of alternate forest management strategies on selected bird species or for entire avian communities. Models vary in their mathematical structure, but typically function by considering tree-by-tree changes over time for an area that corresponds to that of a canopy tree or some sample unit. The spatial scale of these models corresponds to what has been termed the microhabitat scale for birds. Because such simulators have the ability to predict structural changes in the forest through time, one can couple this quantitative data with statistical classification procedures previously mentioned to project long-term consequences of different management practices on available habitat.

Objectives of this research have been 1) to integrate techniques of multivariate classification with the predictive ability of a forest stand simulation model, and 2) to use the resulting model to determine effects of forest management practices on availability of nongame bird habitat. This synthesis requires: a) a structural classification of forest stands in terms of suitability for specific bird species, and b) ability of the forest stand simulator to generate specific variables on which the classification is based. By introducing disturbances (e.g., fire, timber harvest) to the model, we can evaluate effects of natural and man-induced perturbations on availability of habitat for a specific species of bird.

The remainder of this paper will be devoted to presenting an example of this method, FORHAB, a forest stand simulation model designed to predict impacts of certain forest management decisions on availability of habitat for the avian community inhabiting the Walker Branch Watershed.

The Walker Branch Watershed is a 97.5 ha site on the D.O.E. reservation in Anderson County, Tennessee (fig. 2). The watershed ranges in elevation from 285 m to 375 m and occupies an area of steeply sloping ridges and narrow valleys. Girgal and Goldstein (1971), in an analysis of the structure of the watershed, found dominant forest types to be pine (predominately _Pinus echinata_), yellow popular (dominated by _Liriodendron tulipifera_), oak-hickory (mixed _Quercus_ spp., _Carya_ spp.) and chestnut oak (typified by _Quercus prinus_).

MODEL

The following model, FORHAB, is a modified version of FORET (Shugart and West 1977), an Appalachian deciduous forest stand simulator. A detailed description of the model (FORET) can be found in Shugart and West (1977). For the purpose of this paper we will review briefly the general form of the model, but will discuss only modifications in detail.

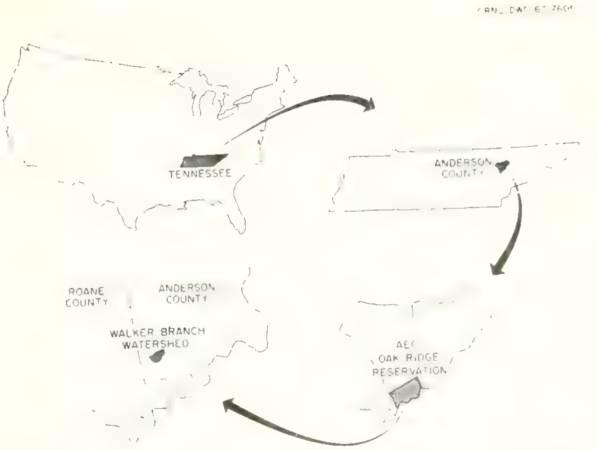

Figure 2. Location of Walker Branch Watershed, Oak Ridge, Tennessee.

FORHAB, like its parent model, simulates the annual change of a forest stand (0.085 ha circular plot) by calculating the growth increment of each tree growing on the stand (subroutine GROW), by tabulating the addition of new saplings to the stand (subroutines BIRTH and SPROUT), and by tabulating the death of trees present on the stand (subroutine KILL). These processes are modeled as stochastic functions. Growth parameters for tree species and climatic conditions included in the model are based on sites of lower slope positions located in eastern Tennessee. A flow chart for FORHAB is provided in appendix I. The main equations for the above subroutines are summarized in appendix II. CUT, HABIT and DISCRM subroutines will be dealt with separately.

Subroutine CUT

The CUT subroutine simulates various forest management practices which are applicable to the southeastern deciduous forest type. The version of this subroutine used for the following analysis was a diameter-limit cut. In this subroutine all commercially valuable species for sawtimber greater than 23 cm dbh (diameter at breast height) were removed from the plot on a 60-year rotation. This form of timber management was practiced on the watershed prior to 1940. The rotation period of 60 years was determined by analysis of stem and basal area curves generated by FORHAB after initial simulations of logging on the watershed.

Subroutine HABIT

The process of classifying stands by their potential to provide habitat for a given bird species is carried out in subroutine DISCRM. The classification is based the following biomass variables which describe vegetational structure of the forest stand:

Foliage biomass of trees 1.2-8.4 cm dbh
Foliage biomass of trees 8.5-22.8 cm dbh
Foliage biomass of trees >22.8 cm dbh
Branch biomass of trees 1.2-8.4 cm dbh
Branch biomass of trees 8.5-22.8 cm dbh
Branch biomass of trees >22.8 cm dbh
Bole biomass of trees 1.2-8.4 cm dbh
Bole biomass of trees 8.5-22.8 cm dbh
Bole biomass of trees >22.8 cm dbh
Number of trees 1.2-8.4 cm dbh
Number of trees 8.5-22.8 cm dbh
Number of trees >22.8 cm dbh
Foliage biomass of average tree 1.2-8.4 cm dbh
Foliage biomass of average tree 8.5-22.8 cm dbh
Foliage biomass of average tree >22.8 cm dbh
Branch biomass of average tree 1.2-8.4 cm dbh
Branch biomass of average tree 8.5-22.8 cm dbh
Branch biomass of average tree >22.8 cm dbh
Bole biomass of average tree 1.2-8.4 cm dbh
Bole biomass of average tree 8.5-22.8 cm dbh
Bole biomass of average tree >22.8 cm dbh

Model output in the form of species and tree diameters must be used to calculate these biomass variables.

The HABIT subroutine divides all trees on the simulated plot into two groups, conifer and deciduous, and then into three size classes within each of these two groups. The foliage, branch and bole biomass for each tree is then calculated using regression equations in table 1, which are site specific to the Walker Branch Watershed (Harris et al. 1973). These values are then summed for all trees on a plot for each size class to provide the variables listed above.

Subroutine DISCRM

The classification of simulated forest stands as potential habitat for a given bird species is carried out in subroutine DISCRM. The classification is based on the statistical procedure of two-group discriminant function analysis (Morrison 1967). Classification criteria were constructed using vegetation data collected on 298 0.085-ha permanent census plots. Breeding territories of various bird species were located and mapped if they either contained or overlapped any of the 298 plots. If a plot was located within the territory of an individual bird (breeding pair), that plot was considered as potential habitat for that species. Conversely, if a given plot was not within the boundary of a territory of an individual of that species, that plot was classified as not providing habitat for that species. Thus data were obtained on areas of both suitable habitat and areas considered inadequate for the needs of the various species. Data on vegetation of these census plots, in the form of species and diameter for each tree on the plot, then were used to generate biomass variables for classification using the same regression equations as those in subroutine HABIT.

Table 1. Uncorrected regressions (ln-ln) of tree component weight (kg) on tree diameter breast height (cm) used in subroutine HABIT.

Dependent variable		Intercept (a)	Slope (b)	R^2	N[1]	K[2]
Leaf	All spp.	-3.498	1.695	0.86	302	1.34
	Hardwoods	-3.862	1.740	0.88	178	
	Conifers	-2.907	1.674	0.91	65	
Branch	All spp.	-3.188	2.226	0.91	298	1.26
	Hardwoods	-3.173	2.224	0.89	231	
	Conifers	-3.461	2.292	0.95	51	
Bole	All spp.	-2.437	2.418	0.97	298	1.08
	Hardwoods	-2.270	2.385	0.98	231	
	Conifers	-3.787	2.767	0.96	51	
Branch-bole	All spp.	-2.126	2.393	0.96	371	

[1] N = Number of samples in each regression

[2] K is the correction factor for bias on logarithmic transformation which is multiplied by exp [ln $\hat{Y}$]

Figure 3 is a hypothetical example of the actual classification procedure in subroutine DISCRM. For each bird species, census plots were placed into one of two groups, suitable habitat or unsuitable habitat, based on the process described above. The two elipses in figure 3 represent two populations of census plots plotted in two-dimensional space (with X1 and X2 being two biomass variables from table 1). These two populations were then subjected to two group discriminant function analysis.

Discriminant function analysis is a statistical procedure for finding a linear combination of the original predictor variables (X1 and X2) which results in the largest difference between the two mean vectors (i.e., maximizes the ratio of among-group to within-group sums of squares). Let us examine the case of two populations, suitable habitat and unsuitable habitat plots, with samples of N1 and N2 independent observations. The populations of P (number of variables) responses are multivariate normal with a common variance-covariance matrix Σ, but different mean vectors μ and μ_2. If $\underline{X}1$ and $\underline{X}2$ are the sample mean vectors for the two groups and S is the pooled estimate of Σ, our intention is to find a coefficient vector $\underline{a}$ of the linear compound $\underline{a}X$ of the responses which will maximize the distance between the two groups in P-dimensional space. It can be shown that

$$\underline{a} = S^{-1}(\underline{X}1 - \underline{X}2);$$

and the general form of the resulting discriminant function is

$$Y = (\underline{X}1 - \underline{X}2)'S^{-1}X$$

with

$$Y_i = a_1X_1 + a_2X_2 + \ldots + a_pX_p$$

(where p is the number of variables in the classification).

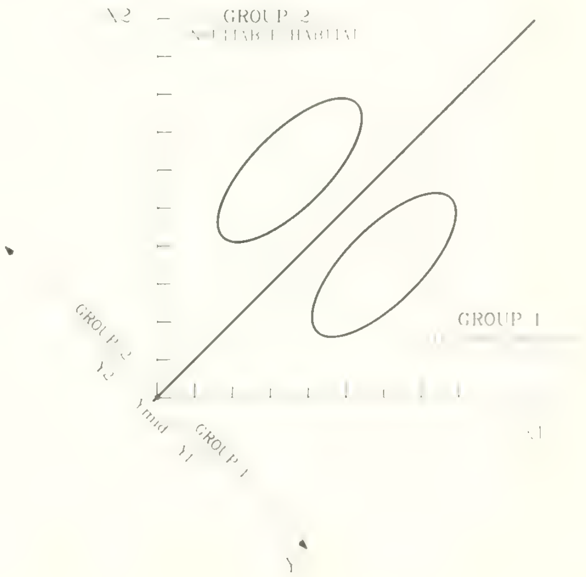

Figure 3. Linear decision scale from subroutine DISCRIM.

In the case of two populations with multivariate normal distributions and respective mean vectors $\underline{X}_1$ and $\underline{X}_2$, common covariance matrix S and prior probabilities of group membership h and (1-h), the Bayes, or minimum expected loss, classification rule states that the observation vector $\underline{X}$ should be assigned to population 1 if

$$\underline{X}'S^{-1}(\underline{\bar{X}}_1-\underline{\bar{X}}_2) - 1/2(\underline{\bar{X}}_1+\underline{\bar{X}}_2)'S^{-1}(\underline{\bar{X}}_1-\underline{\bar{X}}_2) \geq \ln \frac{(1-h)}{h}$$

and assigned to population 2 if this relationship does not hold.

It should be noted that the first term in this equation is the linear discriminant score for the observation vector $\underline{X}$ and the second term is the point midway between the means of the discriminant function as computed for each group or population. For the purpose of classifying simulated observation vectors (subroutine HABIT) the prior probabilities of group membership can be assigned to be equal since there is no a priori reason for assuming group membership. As a result of this assumption, the term to the right of the inequality becomes zero and the equation can be expressed as

$$\underline{X}'S^{-1}(\underline{\bar{X}}_1-\underline{\bar{X}}_2) \geq 1/2(\underline{\bar{X}}_1+\underline{\bar{X}}_2)'S^{-1}(\underline{\bar{X}}_1-\underline{\bar{X}}_2)$$

with the term to the left of the inequality being the discriminant score for the observation vector to be classified and term to the right being the midpoint between the discriminant scores as computed for the group mean vectors.

By calculating the Y_i scores corresponding to the mean vectors $\underline{\bar{X}}1$ and $\underline{\bar{X}}2$ (where X1 = suitable habitat and X2 = unsuitable habitat) and then taking the midpoint of those values;

$$Y_{mid} = (Y1 + Y2)/ 2$$

one can compute the linear decision scale as shown in figure 3.

To classify a newly sampled response (such as a plot output by the model) into either group 1 or 2, the Y_i score must be calculated for that given response vector. If the Y_i value is to the group 1 direction of Y_{mid} then the plot would be classified as belonging to group 1, with the converse holding true if the Y_i value was to the opposite direction of Y_{mid}.

Subroutine DISCRM consists of a series of these linear decision scales, one corresponding to each bird species comprising the avian community on the watershed. Each simulated plot is input to subroutine HABIT where the biomass variables necessary for classification are generated. These variables are then input to subroutine DISCRM where the Y_i value is calculated for that plot. This value is then compared to the Y_{mid} value for each bird species and the decision as to whether that plot provides potential breeding habitat for each of the species of interest is output from the model.

RESULTS

A test of homogeneity of within covariance matrices for the two group discriminant function analysis of ovenbird (Seiurus aurocapillus) habitat found no significant difference between covariance matrices (as approximated by χ^2, $P \geq 0.05$) and they were pooled for the analysis (Kendall and Stuart 1961). The two groups (suitable and unsuitable habitat) were found to be significantly different ($P \geq 0.05$) with respect to those structural variables measured, using the Hotelling T^2 test statistic. Bayesian classification of initial observations (298 plots) based on the two group discriminant function analysis accurately classified group membership (suitable and unsuitable habitat) for 96% of the forested plots, with prior probabilities of group membership being set proportional to the number of observations in each group.

Figure 4 shows results of a 500-year simulation of available habitat for the ovenbird (Seiurus aurocapillus) on Walker Branch Watershed. Results are presented as percentage of total land area which provides potential breeding habitat for the ovenbird over a 500-year period. Year zero represents the present structural configuration of the forest on the watershed. This was accomplished by initializing the model with 25 randomly chosen census plots from the watershed using vegetation data collected on these plots in 1977. Results are given for both simulations including timber management (diameter-limit cut) and undisturbed conditions. Simulations of undisturbed forest dynamics show an initial increase in available habitat for the ovenbird from 20 percent of the land area to approximately 65 percent over the next 60 years. This decline to year 90 is followed by a general oscillation of available habitat from 10 to 20 percent for the remainder of the simulation with only one period of increase above 30 percent, that being at approximately year 250.

In comparison, results of the simulation which included timber management showed considerable divergence from simulations of the undisturbed forest. Dynamics previous to the first cut at year 60 were identical for both managed and undisturbed simulations. Following the first cut at year 60, however, we see a divergence with the managed stands showing an increase in available habitat to 85 percent by year 90 as compared to the 5 percent available habitat for the undisturbed simulations. This increase is followed by a continuous decline over the next 30 years until the second cut at year 120. At this time once again we see an increase in available habitat for the ovenbird to 50

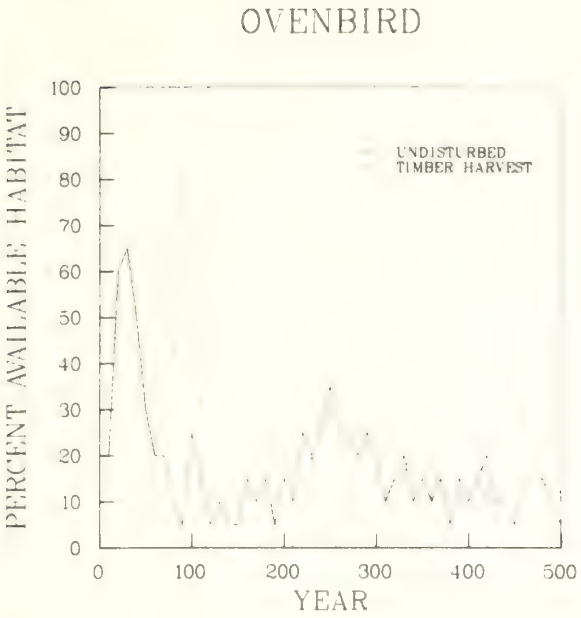

Figure 4. Results from 500-year simulation of ovenbird habitat on the Walker Branch Watershed in east Tennessee. Available habitat expressed as percentage of total land area of the watershed.

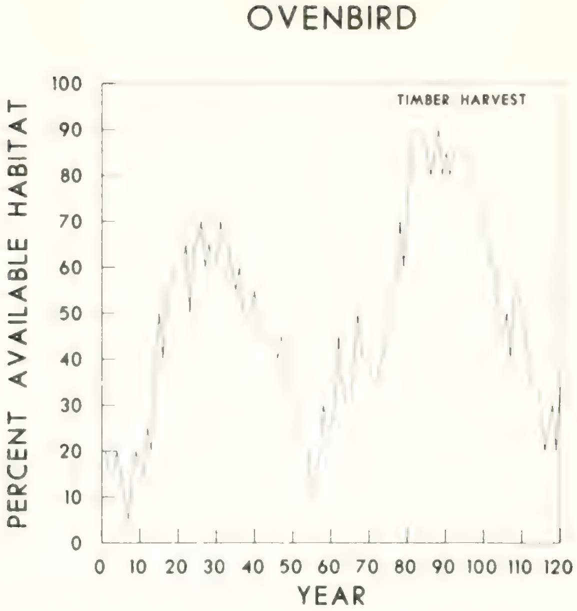

Figure 5. Results from 120 year simulation of available ovenbird habitat on the Walker Branch Watershed under conditions of timber management. Available habitat expressed as percentages of the total land area of the watershed.

percent of the total forested area of the watershed. Following the second timber harvest at year 120 there is a decline in available habitat continuing to the next cut at year 180. Following the third cut there is a continuing decline to year 210, when the model predicts there will be no potential breeding habitat for the ovenbird on the watershed. In all remaining cuts there is an initial increase in available habitat following harvest. This is followed by a decline, which generally continues until the next cut, the last being at year 480.

Figure 5 presents results of the same simulation under conditions of timber management that were presented in figure 4, only over a shorter time scale showing the short-term dynamics of available habitat following timber harvest (year 60). Once again there is an initial increase in availability of suitable habitat followed by a decline at year 30. This decline continues until the forest is cut at year 60, when those trees greater than 23 cm dbh and of commercial value as sawtimber are removed from the forest. This thinning of the forest results in an increase of potential habitat for the ovenbird over the next 35 years, at which time a downward trend begins and continues through the remainder of the simulation.

DISCUSSION

Results presented in Figures 4 and 5 represent predicted dynamics of available habitat for the ovenbird on the Walker Branch Watershed. The 500-year simulation in figure 5 is meant to show that extrapolations cannot necessarily be made from results of a single timber cut to cuts pending in the future. Resulting availability of habitat for the ovenbird following an initial diameter-limit cut on a 60-year rotation may not represent availability of potential habitat the forest will provide following future diameter-limit cuts. Availability of habitat following the first cut increased dramatically, but subsequent cuts on a 60-year rotation yielded quite different results. Secondly, failure to look at potential effects of repeated harvests may mislead the manager with respect to long term habitat dynamics. As can be seen in results of the 500-year simulation, the first cut was followed by a four-fold increase in available habitat for the ovenbird. Subsequent cuts, however, resulted in less dramatic increases and in some cases led to elimination of potential habitat.

These results show the importance of historic considerations in determining effects of particular timber management practice on a given forest. Structural configuration of the forest prior to cutting is of utmost importance in the case of repeated long-term management plans. To date this type of information has been lacking. FORHAB and models of its type can be used to provide information on long-term management plans and combinations of management schemes before their actual implementation.

Results (figs. 4 and 5) show an initial

increase in potential habitat after the initial cut at 60 years. This increase contrasts with decline of habitat availability for undisturbed simulations. The increase after cutting is a result of thinning or general decrease in density of stands on the watershed. At present the forest has gone approximately 70 years without a timber harvest, so by year 60 the stand is approximately 130 years in age. Thinning of larger trees, which leads to an initial increase in available habitat, is quickly followed by an increased density of the understory, reducing available habitat. This is the reason for the pattern of initial increase after cutting followed by a subsequent decline in availability of habitat for the ovenbird. These results are in general agreement with the structure of vegetation chosen as breeding habitat by the ovenbird on the watershed. Optimal habitat for the ovenbird on the Walker Branch Watershed (as determined by the relationship between vegetational structure and prey abundance) is a deciduous stand with a sparse understory and brush and little ground cover.[5]

It should be noted that the model simulates availability of potential breeding habitat expressed as a percentage of the total area under consideration. The model does not simulate population dynamics of a given bird species per se. The ability of the ovenbird population to track changes in availability of habitat such as the initial increase in habitat following the first timber harvest, or to reinvade after the disappearance of potential breeding habitat in an area are not considered explicitly in the model. These considerations would depend on immigration into the area or the existence of a "floater" population of nonbreeding individuals unable to establish territories due to lack of suitable habitat. Likewise, the model does not consider quality of habitat provided by a given stand. Some marginal areas may become potential habitat depending on size of the ovenbird population. These points must be kept in mind when interpreting results of simulation from the model.

The potential of predicting effects of proposed management schemes on habitat availability need not be limited to the breeding season during spring and summer months. For many resident bird species, availability of suitable habitat during fall and winter seasons may be the major limiting factor. Figure 6 shows seasonal variation in habitat selection for several species of birds on the watershed as expressed by the first two discriminant functions describing the vegetational structure of the forest stands (Shugart et al. 1975). It can be seen that in many cases the habitat needs of certain species change seasonally. By including information on seasonal habitat requirements into the classification procedure, FORHAB and models of its type could be used to determine habitat availability not only on a yearly basis, but seasonal variations in available habitat.

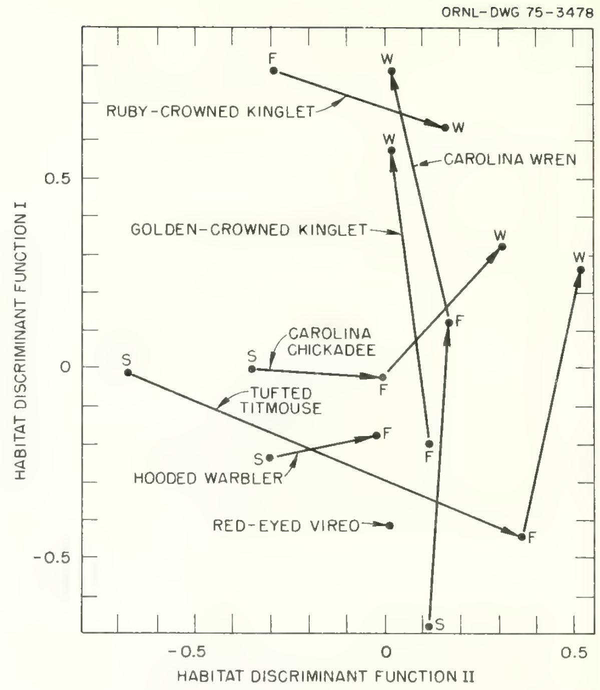

Figure 6. Seasonal variation in habitat selection for several species of birds inhabiting the Walker Branch Watershed.

Two-group discriminant function analysis (as described in subroutine DISCRM) can be used to construct habitat maps which reflect the potential of a site to provide habitat for a given species of bird. A map of potential habitat for five woodpecker species on the Haw Ridge Watershed on the D.O.E. reservation in east Tennessee is shown in figure 7 (Shugart et al. 1978). The map was constructed using a classification scheme identical to that presented for subroutine DISCRM. By initializing the model for a given forested region such as the Haw Ridge Watershed (initial conditions based on sample plots from the Haw Ridge Watershed as was done for the Walker Branch Watershed) it would be possible to construct a series of maps representing changes in available habitat for the area through time. This would aid in more site specific, small scale management problems.

The model FORHAB which has been presented as an example of the process and methodology of habitat simulation has dealt solely with the Appalachian deciduous forest of the Southeast. However, the general form of the forest simulation model underlying this method (FORET) has been adapted for a wide variety of forested areas, including mixed conifer-hardwood forests of the Northeast (Botkin et al. 1972), loblolly pine forests of Arkansas (Milke 1978) and rain forests of Puerto Rico (Doyle 1980). Another version of

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[5] T.M. Smith, unpublished data on file at Oak Ridge National Laboratory.

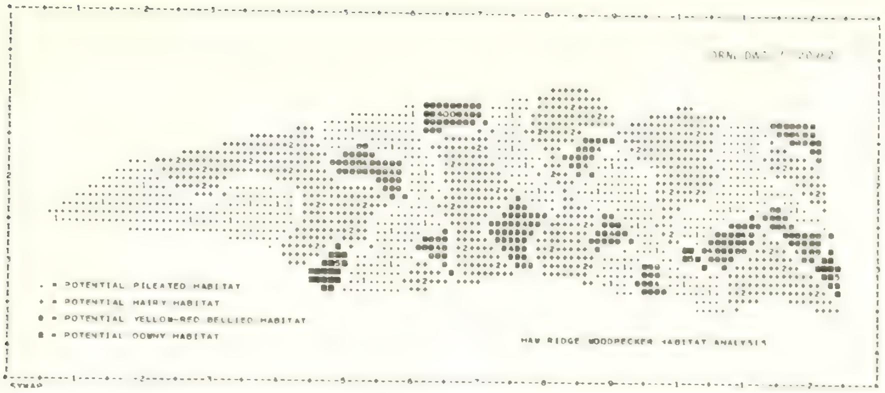
. = POTENTIAL PILEATED HABITAT
+ = POTENTIAL HAIRY HABITAT
● = POTENTIAL YELLOW-RED BELLIED HABITAT
■ = POTENTIAL DOWNY HABITAT
HAW RIDGE WOODPECKER HABITAT ANALYSIS
SYMAP

Figure 7. Map of potential habitat for five species of woodpecker on Haw Ridge as defined by discriminant function classification procedure.

the model FORMIS[6] simulates flood plain forests of the Mississippi River and could be modified to simulate riparian habitats in other areas.

Potential applications of the model to predict effects of proposed and untried management schemes on specific forested areas for both individual species and the avian community as a whole, as well as its versatility and adaptability to a diverse array of forested regions, make models like FORHAB potentially important tools for forest and wildlife managers in the future.

ACKNOWLEDGMENTS

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[6] M.L. Tharp, unpublished model available at Oak Ridge National Laboratory.

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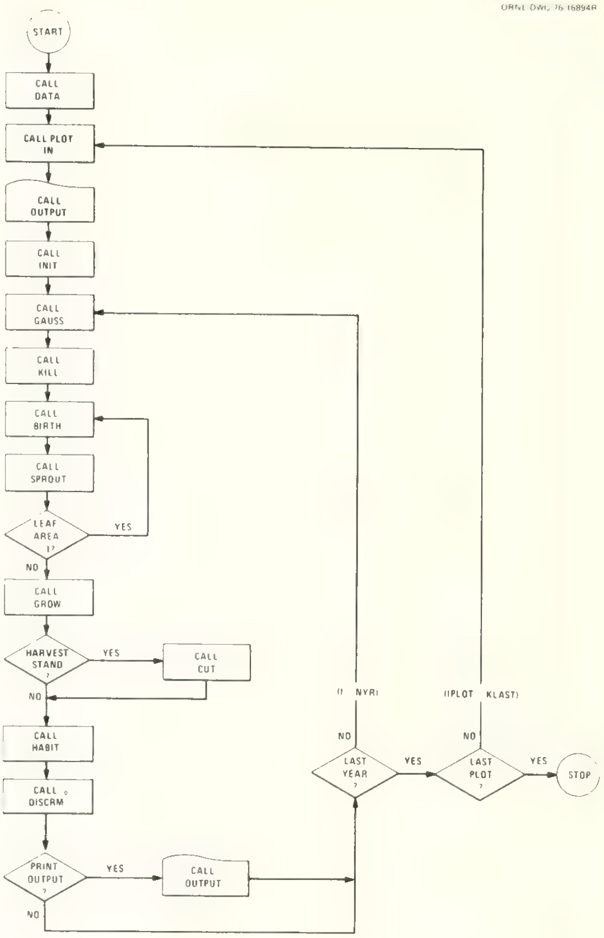
Appendix I. Flow diagram for FORHAB.



Appendix II. Model equations in FORHAB.

Process	Equations
Growth of each tree under optimal conditions[1]	$\frac{d[D^2 H]}{dt} = R\ LA\ (1 - \frac{DH}{D_{max} H_{max}})$ R = growth rate parameter, LA = leaf area of tree, D = diameter at breast height, H = height of tree, D_{max} = maximum diameter for a particular species, H_{max} = maximum height for a particular species, D^2H = index of tree volume.
Height/diameter relation[2]	$H - 137 + b_2 D - b_3 D^2$, $b_2 = 2(H_{max} - 137)/D_{max}$, $b_3 = (M_{max} - 137)/D^2_{max}$, b_2 and b_3 determined by setting $H = H_{max}$ and $dH/dt = 0$ when $D = D_{max}$.
Extinction of light as a function of leaf area in forest canopies[3]	$Q(h) = Q_o \exp(-k \int_h^\infty LA(h')dh')$ LA(h') = distribution of leaf area as a function of height Q_o = incident radiation, Q(h) = radiation at height (h), K = constant[3].
Reduction of photosynthesis due to shading[4]	Various empirical equations fitted to light-photosynthesis curves for shade-tolerant or shade-intolerant species found in each forest. These equations are used to reduce the magnitude of the growth equation (above) for shaded trees.
Crowding effects related to stand biomass (competition)[1]	S(BAR) = 1 - BAR/SOILQ, BAR = total biomass (basal area) of simulated stand, SOILQ = maximum biomass (basal area) recorded.
Intrinsic tree mortality[1]	$p = 1 - (1 - \varepsilon)^n$, p = probability of mortality at year n is chosen such that $p = 0.99$ when $n = AGE_{max}$ (the maximum age for the species).
Mortality of trees with suppressed growth[1]	If growth is less than a critical value for the species, $p = 0.368$.

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[1] Botkin et al. 1972.

[2] Ker and Smith 1955.

[3] Kasanaga and Monsi 1954, Loomis et al. 1967, Perry et al. 1969.

[4] Kramer and Kozlowski 1960.

A WINDSHIELD AND MULTIVARIATE APPROACH TO THE CLASSIFICATION, INVENTORY, AND EVALUATION OF WILDLIFE HABITAT: AN EXPLORATORY STUDY[1]

C.E. Grue[2], R.R. Reid[3], and N.J. Silvy[4]

Abstract.--Techniques are described for evaluating the habitats of breeding mourning dove (Zenaida macroura), and bobwhite (Colinus virginianus) and scaled quail (Callipepla squamata) from within a vehicle. Audio counts of the three species and habitat surveys were conducted on 133 (24 km) transects in Texas in 1976. The linear distance of each habitat type intersecting a transect and the number of structural features within ca. 0.8 km were recorded. Habitat variables, including indices of habitat interspersion and diversity, were analyzed for correlations with audio counts of the three species using stepwise multiple regression. We used discriminant analysis to determine the accuracy of using habitat variables to identify transects supporting below or above average densities of the three species.

Habitat variables accounted for 28 to 87% of the variation in mourning dove call counts, and 60 to 95% and 32 to 93% of the variation in bobwhite and scaled quail whistle counts, respectively. Discriminant analyses correctly classified 78 to 89% of the mourning dove call-count surveys. Comparable values for whistle counts of bobwhite and scaled quail were 71 to 96% and 39 to 98%, respectively. Results suggest techniques developed may be applicable to analyzing the habitat of wildlife species for which transects are used to obtain population estimates.

Key words: Bobwhite quail; discriminant analysis; habitat classification; habitat evaluation; habitat inventory; mourning dove; multiple regression; scaled quail; Texas; windshield approach.

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[1] Texas Agricultural Experiment Station Technical Article 16235. Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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INTRODUCTION

The abundance of wildlife is usually determined by habitat conditions which alter the carrying capacity of the land. These conditions do not remain static. Our understanding of trends in habitat quality and quantity is limited, even for those wildlife species for which habitat needs are generally known. It is, therefore, essential to determine the habitat requirements of wildlife, develop the capability to assess the abundance of critical habitats, and monitor changes in their quantity and quality.

The mourning dove is a species which has not received management commensurate with its popularity as a game bird (Amend 1969, Sandfort 1977). This species has the widest range of any game bird in the United States and is the most important in North America in terms of numbers and hunter harvest (Keeler 1977). Management of mourning doves in the United States, however, has been almost entirely restricted to control of harvest based on fluctuations in breeding populations monitored nationwide by call-count surveys (Dolton 1977). While some breeding populations have decreased (Dolton 1977), hunter harvest has increased to more than 49 million (Keeler 1977). If demand for utilization of the dove resource continues to increase, habitat management may become essential. First steps in initiating management plans will be habitat inventory, analysis, and evaluation. The objective of our study was to develop techniques for evaluating the habitat of breeding mourning dove from a vehicle ("windshield approach"). Texas was well suited for such a study because of its size and habitat diversity (Gould 1975). In addition, we concurrently evaluated habitats of breeding bobwhite and scaled quail using these same techniques to determine if they were applicable to other wildlife species.

METHODS

Our study of habitats of breeding mourning dove and bobwhite and scaled quail in Texas consisted of four steps: classification, inventory, analysis, and evaluation. Classification was defined as identification and placement of habitats into specific habitat types according to established criteria. Inventory was defined as the process by which abundance of a particular wildlife species or habitat parameter was determined along an audio-count transect. We defined analysis as examination of habitat, its types and structural features, and their relationships to audio counts and one another. Evaluation was defined as the process by which habitats were ranked according to estimated densities of the three species they supported. From these data, use of habitat variables to predict audio counts of the three species was examined.

Classification

We developed a method of classifying habitats from within a vehicle. Habitat type was defined as a description of the vegetation of an area consisting of a unique combination of canopy composition and spatial distribution and ground cover height and composition. Our hierarchial habitat classification (fig. 1) was divided horizontally into three major strata. (Figures and tables follow literature cited). The first, "physiognomic class", was used to describe vertical and horizontal distribution of canopy vegetation within a given area (for detailed descriptions, see Grue 1977). The second level subdivided habitats containing trees on the basis of canopy composition (deciduous, coniferous, or mixed) and presence or absence of understory. In the present study, we also separated mesquite (Prosopis spp.) from other deciduous species. In the third level, cropland, pasture, savannah, parkland, desert scrub, woodland, and forest were further divided based on height and/or composition of ground cover. Classification of canopy and ground cover composition and ground cover height was based on relative abundance within each composition and height category. If at least 75% of canopy or ground cover was similar in composition and height, it was considered homogeneous. Canopy or ground cover in which less than 75% was similar in composition was considered mixed.

We also considered structural features within habitat types; structures or characteristics other than height and composition of ground cover, and composition and spatial distribution of canopy, which others (for review, see Grue 1977, Reid 1977) have suggested may be important to breeding dove and quail. Included within this category were the number of fences, shrubrows, windbreaks, powerlines, roads, and railroad rights-of-way, and whether or not these structures paralleled or intersected the call-count transects. The number of edges (an abrupt change in the physiognomy of the vegetation excluding ecotones), permanent water sources, buildings with associated vegetation, washes, livestock feeders and feedlots, gravel pits, irrigation and oil pumps, and presence of snags (dead, defoliated woody shrubs or trees) within 0.8 km of each transect were included. Type of road surface on the survey route (asphalt, gravel, sand, or dirt) and the width of the road shoulder were recorded at each stop.

Inventory

Call-count and whistle-count data for 1976 were obtained for the first 15 (3-min) listening points (stops) located at 1.6 km intervals along each of the 133 Federal and State mourning dove call-count transects in Texas. Call counts were conducted on each transect four times between 20 May and 10 June 1976 by personnel of the Texas Parks and Wildlife Department (Dunks 1976). Quail whistle counts were conducted concurrently on the last three of the four surveys of each transect. Audio-counts are believed to be reliable indices of the relative abundance of breeding dove (Dolton 1977) and quail (Bennitt 1951, Elder 1956, Rosene 1957, Norton et al. 1961, Campbell et al. 1973, Brown et al. 1978) within relatively large areas.

The habitat intersecting the transects was surveyed during this 20-day time period using two vehicles, each with a two-man team (Grue et al. 1976). To reduce error due to differences in observers, trial surveys were conducted as a group along several transects throughout most of Texas; each team worked within different ecological areas (Gould 1975) and one member of each team was designated driver and odometer reader, while the other person classified habitat throughout the study. A team traveled and recorded habitat data on both sides of each transect starting 0.8 km before and ending 0.8 km after each stop. Each of these 1.6 km units was defined as a transect interval. The linear distance of each observation of a habitat type intersecting the survey route, measured to the nearest 0.02 km, and the number of structural features present within 0.8 km (maximum radius of audibility of each species; Davey 1955, Baxter and Wolfe 1973) were also recorded within each transect interval.

Analysis and Evaluation

Habitat variables were analyzed for correlation with audio counts of the three species by transect, statewide, and within ecological areas, using stepwise multiple regression (Barr and Goodnight 1972). Ecological areas of Gould (1975) were selected because call counts were more homogeneous within their boundaries than those of other physiographic divisions of the State (Grue 1977) and have been used by the Texas Parks and Wildlife Department to analyze annual call-count data (Dunks 1976). Call-count and whistle-count data for all surveys considered valid by the Texas Parks and Wildlife Department were included in analyses because variation in audio counts of the three species between surveys was significant (Grue 1977, Reid 1977). Independent variables (habitat variables) entered and remained in models if values for their partial F-statistics were significant ($P<0.05$).

Habitat interspersion and diversity indices were included in all analyses. Interspersion was calculated by summing frequencies of occurrence for each habitat type within the 15 transect intervals. Habitat diversity was calculated for each transect using the Shannon-Weiner Index (Shannon 1948). Transect call counts and whistle counts were equal to the sum of the number of dove and quail heard calling on the 15 stops, respectively.

To determine importance of spatial distribution of the canopy, canopy composition, and ground cover height and composition in predicting audio counts of the three species, we evaluated seven simplifications of our habitat classification. Simplifications corresponded to horizontal strata within the hierarchy of the initial classification from the most complex (habitat type = physiognomic class + canopy composition + ground cover height and composition) to the least complex (habitat type = physiognomic class). Simplifications were evaluated for each of the three species by ecological area using transect audio counts and habitat variables. Structural features were excluded from stepwise multiple regression analyses so that multiple correlation coefficients represented differences between habitat classifications. Indices for habitat interspersion and diversity were also not included because of the number of simplifications examined. The simplified habitat classification with the fewest habitat variables which also resulted in high multiple correlation coefficients statewide was judged the "best" classification system for each species.

We developed an index to minimum habitat interspersion applicable to the simplified habitat classifications selected. Habitat interspersion was more difficult to calculate than habitat diversity (we continued to use the Shannon-Wiener Index) because the number of times the habitat types actually changed on both sides of a call-count transect was not known. The new interspersion index was based on the number of habitat types present within a transect as well as the presence or absence of each habitat type within adjacent transect intervals. If a particular habitat type was present within a transect interval but was absent within an adjacent interval, the value of the interspersion index increased by 1. Conversely, if a particular habitat type was present or absent within two adjacent transect intervals, interspersion was equal to 0 and the value of the index remained unchanged. This process was continued until all habitat types were examined within the 15 transect intervals of each of the 133 call-count transects. The interspersion index on a particular transect was equal to this value plus the number of habitat types present within the transect. The latter was used as an indirect measure of minimum interspersion within the transect intervals.

We used discriminant analysis (Barr and Goodnight 1972) to determine the accuracy of predicting audio-count classes of the three species using the habitat variables within the simplified habitat classifications selected. Analyses were conducted by ecological area and only those habitat parameters within the multiple linear regression models for a given ecological area were included. A mean transect audio-count was determined for each species and ecological area using data from all call-count and whistle-count surveys conducted in 1976 (table 1). Transect audio counts for each species and survey were then classified into one of two classes: average or above, or below average. The use of habitat variables to predict audio-count classes was evaluated in terms of percent of call-count and whistle-count surveys correctly classified within each class by the discriminant functions. Multiple analysis of variance (Barr and Goodnight 1972) was used to test for statistically significant (P<0.05) differences in values for the habitat variables between the two audio-count classes.

RESULTS

Habitat variables within the initial habitat classification accounted for up to 87% of variation in mourning dove call counts, and up to 94 and 93% of variation in bobwhite and scaled quail whistle counts, respectively (table 2). Analyses within ecological areas resulted in an increase in multiple correlation coefficients and/or a decrease in the number of independent variables in the models. Both habitat types and structural features accounted for a significant portion of variation in audio counts of the three species (table 3).

Simplification of the initial habitat classification resulted in a significant reduction in the number of habitat types, but a relatively slight decrease in multiple correlation coefficients (table 4). The number of habitat types within the simplified habitat classification selected for each of the three species was reduced 90 to 96%, while multiple correlation coefficients decreased by only 4 to 14%. Of seven simplified habitat classifications evaluated, physiognomic class with canopy composition and cropland divisions of grain, nongrain, forage, and plowed ground accounted for the most variation in mourning dove call counts. Physiognomic class with canopy composition with mesquite was the simplified habitat classification selected for both species of quail.

Models for predicting audio counts of the three species incorporating both structural features and habitat types within the simplified habitat classifications selected are presented in table 5. Multiple correlation coefficients for these models were similar to those associated with the initial habitat classification (table 2). Models accounted for 28 to 88% of variation in mourning dove call counts, and 60 to 95% and 32 to 93% of variation in bobwhite and scaled quail whistle counts, respectively, within the 10 ecological areas.

Discriminant functions incorporating the habitat variables within these models correctly classified 75 to 89% of mourning dove call-count surveys within each ecological area into the two audio-count classes (table 6). Comparable values for whistle-count surveys of bobwhite and scaled quail were 71 to 96% and 39 to 98%, respectively (table 6). Multiple analyses of variance indicated that there were significant (P<0.05) differences between values for the habitat parameters within the discriminant functions for the two audio-count classes for each species.

DISCUSSION

Results suggested that the habitat classification and techniques we employed may identify habitat variables significantly correlated with audio counts of mourning dove and bobwhite and scaled quail. Both habitat types and structural features appeared to be important components of habitats selected by the three species during the breeding season. Analyses by transect within ecological areas usually resulted in an increase in multiple correlation coefficients or a decrease in the number of independent variables in models for the three species. These trends may be explained by increased homogeneity in audio counts (Foote et al. 1958) or habitat within ecological areas (Blankenship et al. 1971). Analysis within ecological areas may also more accurately describe the relationships between audio counts of the three species and habitat variables. Simple correlation analyses (Grue 1977; Reid et al. 1978, 1979) suggested audio counts of the three species were correlated with habitat variables that may have provided requisites necessary for survival and reproduction. Habitat parameters which provided these requisites differed between ecological areas and appeared to depend on the abundance and distribution of the habitat types and structural features present. For example, mourning dove call counts were positively correlated with cropland within the Trans-Pecos, but were negatively correlated with this habitat type on the High Plains. In the Trans-Pecos, nesting substrate was abundant, whereas sources of food and water were generally restricted to cultivated areas. The opposite was true on the High Plains, where food and water were more abundant, but nest sites within woody vegetation were limited. Results suggest future analyses and evaluations should be conducted within physiographic divisions.

With a few exceptions, the amount of variation in audio counts of the three species accounted for by habitat types within the initial and simplified habitat classifications selected was similar. Exclusion of mesquite as a separate canopy type from the simplified habitat classification selected for mourning dove may account for the low multiple correlation coefficient associated with models for the South Texas Plains and Rolling Plains. Selection of mesquite habitats by nesting doves on the Rolling Plains has been reported (Jackson 1940). Inclusion of mesquite as a separate canopy type appears to be important in evaluating the habitat of nesting mourning doves within these ecological areas, as well as habitats of both species of quail throughout most of Texas during the breeding season. Similarly, absence of ground cover characteristics within the simplified habitat classification selected for bobwhite and scaled quail may have resulted in low multiple correlation coefficients associated with models for the Edwards Plateau, Rolling Plains, and High Plains, ecological areas in which overgrazing or cultivation was extensive. Ground cover height and composition, however, appear not to be as important as the spatial distribution and composition of the canopy in evaluating habitats of the three species during the breeding season in Texas.

Results of multiple regression and discriminant analyses suggest that habitat variables might be used to predict audio counts of the three species and identify areas supporting above or below average densities within most of the ecological areas of Texas. Reasons for the low multiple correlation coefficients associated with models for mourning dove call counts within the Gulf Prairies and Marshes and scaled quail whistle counts within the Trans-Pecos are not known. High habitat heterogeneity in conjunction with low and uniform mourning dove call counts within the Gulf Prairies and Marshes (Grue 1977) may account for the low multiple correlation coefficient for this model. Conversely, habitat on transects within the Trans-Pecos was relatively homogeneous while whistle counts of scaled quail varied (Reid 1977), suggesting our habitat classification may not have included an important component of the habitat which this species selected for nesting.

Several improvements may be useful in testing and applying the techniques presented. Two improvements could be made in methods used to inventory habitat parameters. Habitat data could be collected using "mark-sense" computer data forms which would eliminate manual transfer of data to computer cards. Collection of habitat data in the sequence observed would permit direct calculation of habitat interspersion at any level within the habitat classification. In addition, aerial photographs and satelite imagery may facilitate inventory of habitat data, particularly within remote areas.

Data analysis could be improved by increasing the number of transects within physiographic units so that the number of observations exceeds the number of habitat types within the habitat classification selected. In the present study, we included audio-count data for all surveys conducted on the 133 call-count transects because differences in audio counts between surveys were significant. By including variation in call counts between surveys, high multiple correlation coefficients were more difficult to obtain (Grue 1977). However, inclusion of multiple surveys of individual transects artificially increased sample sizes within ecological areas, as surveys of the same transect were not statistically independent.

Limitations of stepwise multiple regression analyses should also be considered. Habitat parameters within models may not be the only ones significantly correlated with density. In addition, individual regression coefficients may depend on other variables within a model. Examination of correlation matrices may, therefore, prove useful in 1) identifying all habitat variables significantly correlated with density of the three species, 2) identifying habitat variables which may be more easily inventoried than those within the models and substituted without a significant reduction in multiple correlation coefficients, and 3) establishing guidelines for improving habitat for nesting mourning dove and bobwhite and scaled quail.

Use of the techniques presented to predict fluctuations in wildlife density and evaluate and manage wildlife habitat are outlined in figure 2. Procedures may be divided into three stages: 1) development of multiple linear regression models and discriminant functions which account for the greatest amount of variation in density indices and classes, respectively, and identification of habitat parameters significantly correlated with density of the wildlife species of interest; 2) testing of multiple linear regression models and discriminant functions; and 3) use of models to predict fluctuations in wildlife density, or use of discriminant functions and simple correlation analyses to evaluate and manage wildlife habitat. Procedures within the first stage have already been discussed here and elsewhere (Grue 1977, Reid 1977, Reid et al. 1978, 1979).

Multiple linear regression models may be tested by inventorying habitat parameters and the wildlife species of interest simultaneously on transects within the physiographic unit the models represent and comparing predicted densities and their confidence limits with observed values through time. If predicted and observed densities remain similar over time (i.e., habitat condition is the major factor governing fluctuations in density), the model(s) may be used to predict fluctuations in density. However, if predicted and observed densities differ significantly over time, other environmental factors (e.g., weather, disease, hunting) may be governing fluctuations in the density of species.

Discriminant functions should be tested by inventorying both habitat parameters and wildlife species of interest on additional transects within the physiographic unit for which each function was developed. If the percentage of the test transects correctly classified into each density class is high, the functions may be used to evaluate the habitat intersecting other transects within the physiographic unit for which they were developed. In areas for which the predicted density class of the wildlife species of interest is low, management recommendations could be made to increase those habitat parameters positively correlated with density of the species.

CONCLUSIONS

We believe the habitat classification and techniques described may be applicable to evaluating habitats of breeding mourning dove and bobwhite and scaled quail throughout their ranges, and habitats of other wildlife species for which line transects are used to collect population data. Methods presented may prove useful in predicting annual fluctuations in wildlife density, in determining effects of habitat modification on wildlife density, and in evaluating and managing wildlife habitat. Further research into development and testing of a windshield approach to the evaluation of wildlife habitat is needed and appears justified.

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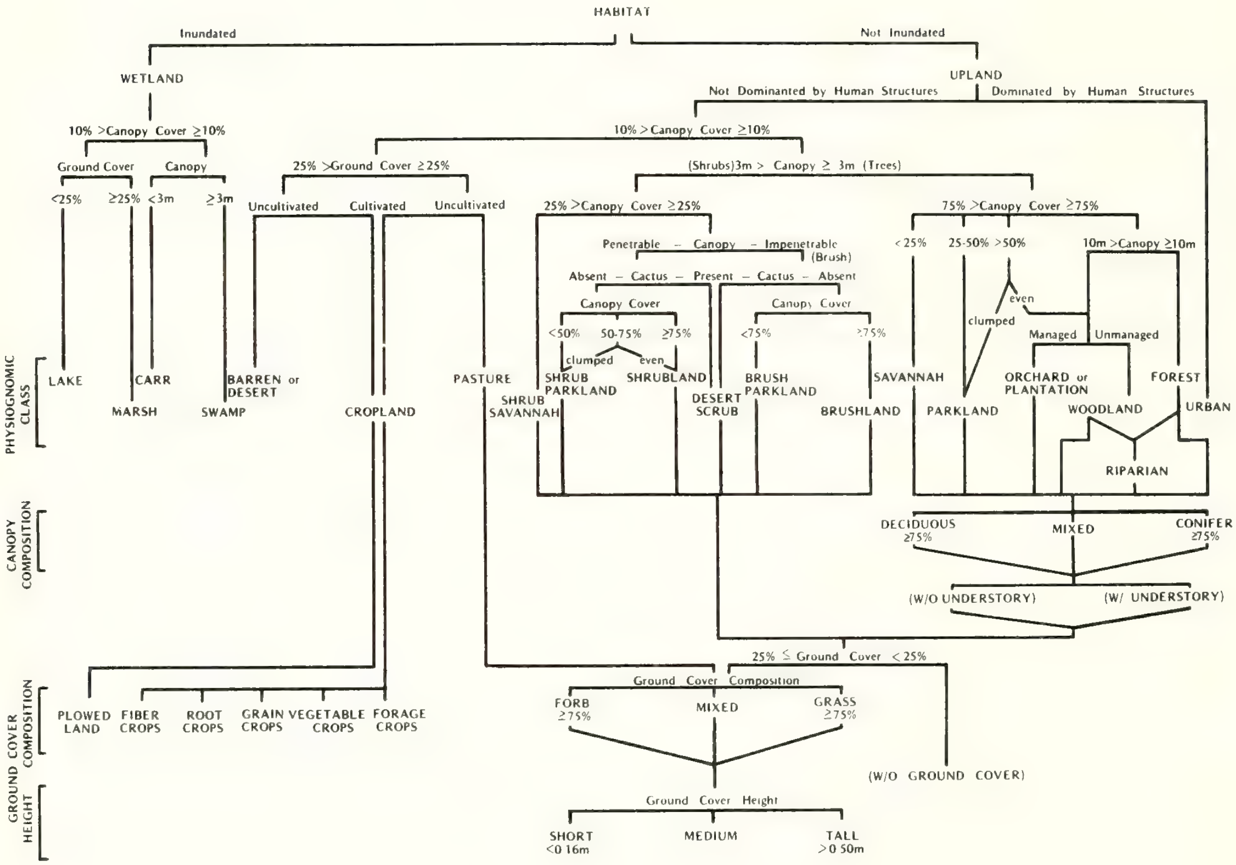


Figure 1. Schematic diagram of habitat classification (after Grue et al. 1976). Habitats were keyed to habitat types from top to bottom. Names were assigned habitat types from bottom to top using words in bold capital letters describing the height and compostion of the ground cover, composition of the canopy, and the physiognomic class, in that order (e.g., tall grass deciduous savannah). Words in brackets specifying the presence or absence of ground cover or understory comprised the last portion of the name for habitat types where appropriate (e.g., mixed woodland with understory).

Table 1. Mean transect audio counts for mourning dove (MD), bobwhite quail (BW), and scaled quail (SQ) within the 10 ecological areas of Texas in 1977. Means are rounded to nearest whole bird. N represents the number of valid surveys conducted.

	MD			BW			SQ		
Ecological area	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
Pineywoods	32	10	7.4	23	13	12.8	23	0	--
Gulf Prairies and Marshes	18	7	3.8	13	43	16.4	13	0	--
Post Oak Savannah	33	17	13.2	24	30	19.5	24	0	--
Blackland Prairies	40	17	9.5	28	29	13.2	28	0	--
Cross Timbers and Prairies	62	27	21.3	44	46	27.7	44	0	--
South Texas Plains	70	28	17.6	52	27	18.9	52	2	3.8
Edwards Plateau	72	18	12.7	54	12	15.6	54	5	8.3
Rolling Plains	88	45	26.3	64	38	20.4	64	4	7.1
High Plains	52	7	7.9	38	6	8.2	38	3	4.7
Trans-Pecos	35	16	18.9	26	0		26	10	5.0

Table 2. Correlations between audio counts of mourning dove (MD), bobwhite quail (BW), and scaled quail (SQ) and habitat variables including habitat types within the initial habitat classification and structural features. Multiple correlation coefficients are expressed as a percent. The number of variables remaining in the models is given in parentheses.

Ecological area	No. habitat variables present	MD	BW	SQ
Pineywoods	98	83.3 (3)	91.1 (3)	
Gulf Prairies and Marshes	96	28.3 (1)	82.2 (2)	
Post Oak Savannah	126	85.9 (3)	94.3 (4)	
Blackland Prairies	105	68.1 (3)	58.9 (3)	
Cross Timbers and Prairies	145	79.3 (6)	83.6 (5)	
South Texas Plains	117	78.2 (4)	93.9 (8)	92.6 (4)
Edwards Plateau	66	64.1 (6)	85.7 (6)	92.9 (5)
Rolling Plains	92	73.5 (10)	89.2 (10)	78.1 (4)
High Plains	52	62.9 (2)	93.8 (5)	81.7 (4)
Trans-Pecos	36	86.5 (3)		31.9 (1)
Texas	194	79.8 (54)	89.5 (51)	65.8 (16)

Table 3. Correlations between transect audio counts of mourning dove (MD), bobwhite (BW), and scaled quail (SQ) and habitat variables considering structural features and habitat types within the initial habitat classification, separately. Multiple correlation coefficients are expressed as percents. The number of variables remaining in the models is given in parentheses.

	Structural features				Habitat types			
Ecological area	Number present	MD	BW	SQ	Number present	MD	BW	SQ
Pineywoods	19	80.2(3)	91.1(5)		75	83.2(3)	91.1(3)	
Gulf Prairies and Marshes	19	28.3(1)	80.0(2)		73	22.8(1)	82.2(2)	
Post Oak Savannah	20	87.0(4)	80.7(2)		102	85.9(3)	94.9(5)	
Blackland Prairies	20	47.5(1)	46.2(2)		81	70.8(4)	58.9(3)	
Cross Timbers and Prairies	20	78.4(10)	65.5(5)		121	79.3(6)	83.5(6)	
South Texas Plains	22	70.2(8)	76.1(6)	92.6(3)	91	78.2(4)	94.3(9)	92.7(5)
Edwards Plateau	16	32.7(4)	54.7(6)	44.8(3)	47	64.3(6)	83.6(5)	93.2(10)
Rolling Plains	19	47.7(5)	40.9(5)	44.8(3)	70	72.1(10)	86.5(10)	78.0(4)
High Plains	17	51.3(4)	75.2(4)	74.7(3)	32	62.9(2)	93.5(5)	81.7(4)
Trans-Pecos	16	84.1(3)		31.9(1)	17	81.5(2)		30.0(1)
Mean	19	60.7(4)	67.8(4)	57.8(3)	71	70.1(4)	85.4(5)	75.1(5)

Table 4. Correlations between transect audio counts of mourning dove, bobwhite quail, and scaled quail and habitat types within simplified habitat classifications. Multiple correlation coefficients are expressed as percents; those underlined represent the habitat classification scheme selected as 'best.' The number of potential habitat types within each classification scheme is given in parentheses.

			Physiognomic class						
						w/canopy composition			
								w/understory	
		Initial		w/mesquite		w/crops	w/mesquite		w/crops
Species	Ecological area	(501)	(19)	(33)	(29)	(34)	(43)	(44)	(49)
Mourning Dove	Pineywoods	83.2	83.3	83.3	82.9	82.9	82.9	82.2	82.2
	Gulf Prairies & Marshes	22.8	0.0	0.0	0.0	22.8	0.0	0.0	22.8
	Post Oak Savannah	85.9	86.7	85.8	87.6	85.9	84.5	85.5	85.9
	Blackland Prairies	70.8	70.0	71.0	70.2	70.2	65.2	69.3	56.2

(continued)

(table 4 continued)

	Cross Timbers & Prairies	79.3	61.9	68.9	71.7	78.4	79.1	73.1	79.0
	South Texas Plains	78.2	35.0	74.3	28.2	60.5	75.6	29.3	60.4
	Edwards Plateau	64.3	42.6	42.6	55.1	55.1	57.8	55.1	55.1
	Rolling Plains	72.1	35.8	40.1	36.4	36.4	50.2	36.4	36.4
	High Plains	62.9	64.0	64.0	64.0	63.9	64.0	64.0	64.0
	Trans-Pecos	81.5	80.7	24.3	80.7	81.5	24.3	80.7	81.5
	Mean	70.1	56.0	55.4	57.6	63.8	58.4	57.6	62.3
Bobwhite Quail	Pineywoods	91.1	90.6	90.6	88.7	88.7	88.7	90.2	90.2
	Gulf Prairies & Marshes	82.2	79.3	81.9	80.5	69.3	81.9	80.4	69.3
	Post Oak Savannah	94.9	92.2	87.9	94.2	94.4	89.0	94.2	88.4
	Blackland Prairies	58.9	0.0	63.7	59.4	16.6	64.7	52.9	38.5
	Cross Timbers & Prairies	83.5	0.0	58.7	0.0	60.2	79.1	0.0	60.2
	South Texas Plains	94.4	68.8	69.4	68.1	79.8	94.7	68.1	79.8
	Edwards Plateau	83.6	75.3	79.7	75.6	75.6	81.5	75.6	75.6
	Rolling Plains	86.5	46.4	72.5	50.2	57.1	70.3	52.8	52.8
	High Plains	93.5	75.5	75.4	75.5	80.0	72.4	88.6	88.6
	Mean	85.4	58.7	75.5	65.8	69.1	80.3	67.0	71.5
Scaled Quail	South Texas Plains	92.7	19.5	70.1	19.5	19.5	85.3	19.5	19.5
	Edwards Plateau	93.2	44.6	36.9	44.6	44.6	42.0	44.6	44.6
	Rolling Plains	78.0	58.7	67.3	58.7	58.7	67.3	58.7	58.7
	High Plains	81.7	66.2	81.7	66.2	74.6	81.7	70.3	74.4
	Trans-Pecos	30.0	0.0	30.0	0.0	15.5	30.0	0.0	15.5
	Mean	75.1	37.8	57.2	37.8	42.5	61.3	38.6	42.5

Table 5. Multiple linear regression models for transect audio counts of mourning dove (MD), bobwhite quail (BW), and scaled quail (SQ) and habitat variables including habitat types within the simplified habitat classifications selected and structural features. Multiple correlation coefficients are expressed as percents.

Ecological Area	Model	R^2
Pineywoods	MD = -0.4 + 0.8[PARALLEL SHRUBROWS] - 4.0[DECIDUOUS FOREST] + 0.4[PARALLEL POWERLINES]	81.3
	BW = -15.7 + 12.4[DECIDUOUS SAVANNAH] + 9.5[DECIDUOUS FOREST] +0.3[PARALLEL FENCES]	90.9
Gulf Prairies & Marshes	MD = 1.3 + 0.1[INTERSECTING FENCES]	28.3
	BW = 22.5 + 41.5[SAND ROAD SURFACE] + 18.2[SHRUB SAVANNAH]	82.0
Post Oak Savannah	MD = 28.0 + 18.8[HAY] - 7.0[GRAVEL PITS] + 10.3[SHRUB PARKLAND] - 1.4[PASTURE OR FIELDS]	87.5
	BW = 11.6 + 54.5[MESQUITE WOODLAND] + 33.9[MIXED MESQUITE SHRUB PARKLAND] + 101.6[CONIFER PARKLAND] + 307.4[ORCHARDS]	93.8
Blackland Prairies	MD = 55.6 - 1.1[INTERSECTING ROADS] + 86.7[ORCHARDS] -0.1[BUILDINGS AND ASSOCIATED VEGETATION]	68.1
	BW = 19.6 - 99.1[MESQUITE SHRUB SAVANNAH] + 0.5[BUILDINGS AND ASSOCIATED VEGETATION] + 1.1[PARALLEL POWERLINES]	60.1
Cross Timbers & Prairies	MD = 98.8 + 6.1[GRAVEL PITS] - 0.3[INTERSECTING FENCES] + 6.8[DECIDUOUS WOODLAND] - 5.0[WASHES] + 108.4[CONIFER PARKLAND] - 37.0[HABITAT DIVERSITY] + 3.4[PLOWED LAND]	71.5
	BW = 611.8 + 22.5[PARALLEL FENCES] - 181.7[BARREN LAND] - 59.3[SHRUB PARKLAND] + 0.8[ROAD SHOULDER WIDTH] + 5.8 [GRAVEL PITS] - 259.2[MIXED MESQUITE SHRUBLAND] + 34.3[MIXED MESQUITE SHRUB SAVANNAH]	77.9
South Texas Plains	MD = 7.6 + 19.5[HAY] - 4.9[PASTURE OR FIELDS] + 2.2[SNAGS] - 0.6[INTERSECTING SHRUBROWS] + 14.8[HABITAT DIVERSITY] - 2.1[DECIDUOUS PARKLAND]	74.7
	BW = 12.0 + 5.1[MESQUITE PARKLAND] + 12.0[HABITAT DIVERSITY] - 2.0[GRAVEL ROAD SURFACE] + 3.0[LIVESTOCK FEEDERS] + 5.0[BRUSHLAND] + 5.9[INTERSECTING RAILROADS] + 0.4[BRUSH W/MESQUITE] + 5.7[DECIDUOUS WOODLAND] + 1.0[MIXED MESQUITE SHRUBLAND] + 0.4[PARALLEL POWERLINES]	95.0
	SQ = 8.9 - 0.2[INTERSECTING POWERLINES] + 0.3[PARALLEL WINDBREAKS] + 4.1[URBAN DEVELOPMENT] - 1.8[INTERSECTING RAILROADS] - 2.9[IRRIGATION PUMPS] + 2.6 [BRUSHLAND] - 0.2[ROAD SHOULDER WIDTH] - 1.5[DECIDUOUS SAVANNAH] - 0.3 [MESQUITE PARKLAND] + 0.2[ASPHALT ROAD SURFACE] + 0.3[SHRUBLAND]	93.1
Edwards Plateau	MD = 2.9 + 14.5[URBAN DEVELOPMENT] + 4.3[BRUSHLAND] + 4.9[MIXED PARKLAND] + 2.9 [PASTURE OR FIELDS] + 0.3[INTERSECTING FENCES] - 1.1[MIXED WOODLAND] + 5.2 [INTERSECTING RAILROADS]	63.9
	BW = 1.9 + 7.6[BRUSHLAND] + 3.8[DECIDUOUS SAVANNAH] + 2.2[MESQUITE WOODLAND] - 1.9[MESQUITE SHRUBLAND]	81.5
	SQ = 7.2 - 3.9[HABITAT DIVERSITY] + 6.5[SHRUB SAVANNAH] + 17.3[INTERSECTING RAILROADS] + 0.4[SHRUBLAND] - 1.0[WASHES] - 0.7[INTERSECTING ROADS] + 0.4 [DECIDUOUS SAVANNAH] + 0.1[PARALLEL POWERLINES]	93.3

(continued)

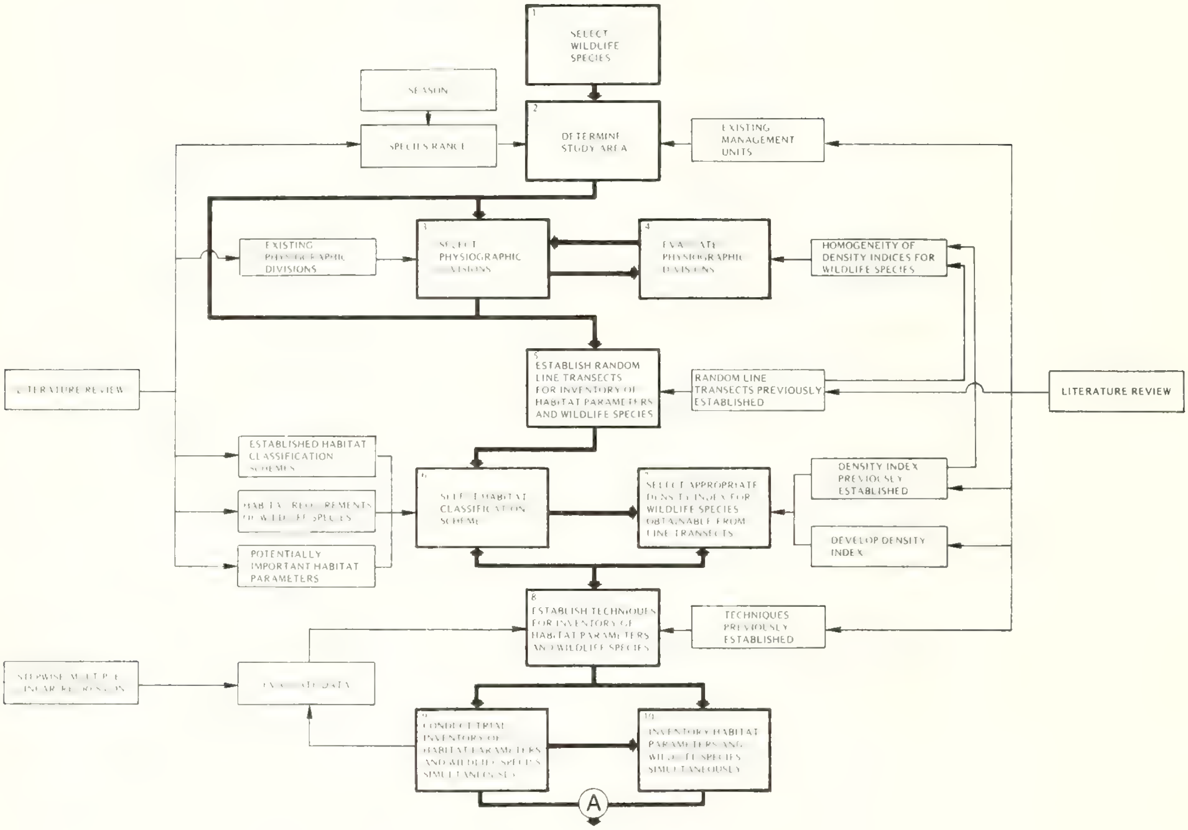
(table 5 continued)

Rolling Plains	MD = 2.1 + 3.4[DECIDUOUS PARKLAND] + 2.0[SNAGS] + 26.0[HABITAT DIVERSITY] - 3.3 [PARALLEL WINDBREAKS]	55.7
	BW = - 18.6 + 66.8[HABITAT DIVERSITY] + 33.1[MESQUITE SHRUB PARKLAND] + 4.1 [INTERSECTING WINDBREAKS] - 1.7[INTERSECTING ROADS] - 2.3[MESQUITE SAVANNAH] + 98.3[CONIFER SAVANNAH] + 3.4[BUILDINGS AND ASSOCIATED VEGETATION] - 2.7 [INTERSECTING POWERLINES] - 371.1[ORCHARDS] + 198.4[CONIFER PARKLAND] +3.1[MESQUITE PARKLAND] - 5.9[MIXED MESQUITE PARKLAND] + 56.2[DECIDUOUS WOODLAND] - 1.3[HABITAT INTERSPERSION]	87.4
	SQ = - 4.5 + 2.1[WASHES] + 4.2[SHRUB PARKLAND] - 11.3[MESQUITE SHRUBLAND] + 0.4 [PARALLEL POWERLINES] + 3.8[MESQUITE SHRUB PARKLAND] + 1.7[INTERSECTING RAILROADS]	75.4
High Plains	MD = 0.3 + 71.9[DECIDUOUS SAVANNAH] + 0.7[PASTURE OR FIELDS]	63.9
	BW = 3.0 + 62.8[SHRUBLAND] + 0.9[GRAVEL ROAD SURFACE] - 32.0[SHRUB PARKLAND] + 0.3[BUILDINGS AND ASSOCIATED VEGETATION] - 0.6[ROAD SHOULDER WIDTH] - 3.3 [MESQUITE SHRUB SAVANNAH]	92.6
	SQ = 0.7 + 25.7[MESQUITE SHRUBLAND] + 74.8[SHRUB SAVANNAH] + 33.2[SHRUB PARKLAND] + 4.7[URBAN DEVELOPMENT]	81.7
Trans-Pecos	MD = 16.1 + 23.5[PLOWED LAND] - 4.7[BUILDINGS AND ASSOCIATED VEGETATION] - 0.5 [HABITAT INTERSPERSION]	86.6
	SQ = 8.9 + 0.6[IRRIGATION AND OIL PUMPS]	31.9

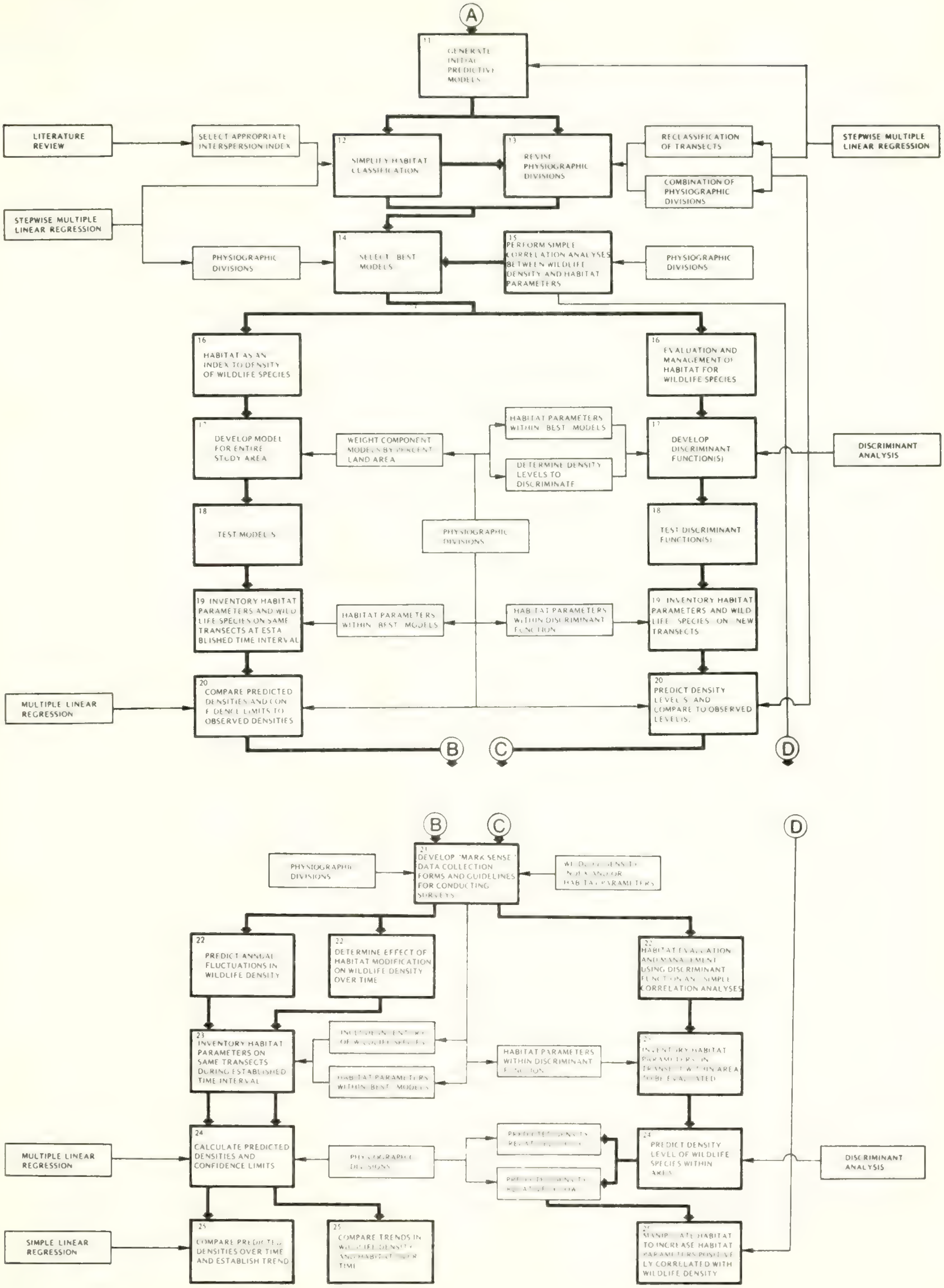
Table 6. Percent audio-count surveys of mourning dove (MD), bobwhite quail (BW) and scaled quail (SQ) correctly classified as below average or average and above by discriminant analyses. Discriminant functions incorporated the habitat variables within multiple linear regression models for each ecological area (see table 5); differences in habitat variables between audio-count classes were significant (MANOVA: P<0.05). N represents the number of audio count surveys.

Ecological area	MD			BW	SQ
	N	%	N	%	%
Pineywoods	32	81.3	23	95.7	
Gulf Prairies and Marshes	18	77.8	13	84.6	
Post Oak Savannah	33	84.8	24	70.8	
Blackland Prairies	40	82.5	28	82.1	
Cross Timbers and Prairies	62	85.5	44	90.9	
South Texas Plains	70	84.3	52	94.2	96.2
Edwards Plateau	72	77.8	54	74.1	98.1
Rolling Plains	88	79.5	64	95.3	93.8
High Plains	52	75.0	[illegible]	89.5	89.5
Trans-Pecos	35	88.6	26		38.5
Mean		81.7		86.4	83.2

Figure 2. Flow diagram for the development, testing, and use of a windshield approach to the evaluation of wildlife habitat.


1
SELECT WILDLIFE SPECIES
SEASON
SPECIES RANGE
2
DETERMINE STUDY AREA
EXISTING MANAGEMENT UNITS
EXISTING PHYSIOGRAPHIC DIVISIONS
3
SELECT PHYSIOGRAPHIC DIVISIONS
4
EVALUATE PHYSIOGRAPHIC DIVISIONS
HOMOGENEITY OF DENSITY INDICES FOR WILDLIFE SPECIES
LITERATURE REVIEW
5
ESTABLISH RANDOM LINE TRANSECTS FOR INVENTORY OF HABITAT PARAMETERS AND WILDLIFE SPECIES
RANDOM LINE TRANSECTS PREVIOUSLY ESTABLISHED
LITERATURE REVIEW
ESTABLISHED HABITAT CLASSIFICATION SCHEMES
HABITAT REQUIREMENTS OF WILDLIFE SPECIES
POTENTIALLY IMPORTANT HABITAT PARAMETERS
6
SELECT HABITAT CLASSIFICATION SCHEME
7
SELECT APPROPRIATE DENSITY INDEX FOR WILDLIFE SPECIES OBTAINABLE FROM LINE TRANSECTS
DENSITY INDEX PREVIOUSLY ESTABLISHED
DEVELOP DENSITY INDEX
8
ESTABLISH TECHNIQUES FOR INVENTORY OF HABITAT PARAMETERS AND WILDLIFE SPECIES
TECHNIQUES PREVIOUSLY ESTABLISHED
STEPWISE MULTIPLE LINEAR REGRESSION
EVALUATE DATA
9
CONDUCT TRIAL INVENTORY OF HABITAT PARAMETERS AND WILDLIFE SPECIES SIMULTANEOUSLY
10
INVENTORY HABITAT PARAMETERS AND WILDLIFE SPECIES SIMULTANEOUSLY
A

(figure 2 continued)


A
11 GENERATE INITIAL PREDICTIVE MODELS
LITERATURE REVIEW
SELECT APPROPRIATE INTERSPERSION INDEX
12 SIMPLIFY HABITAT CLASSIFICATION
13 REVISE PHYSIOGRAPHIC DIVISIONS
RECLASSIFICATION OF TRANSECTS
COMBINATION OF PHYSIOGRAPHIC DIVISIONS
STEPWISE MULTIPLE LINEAR REGRESSION
STEPWISE MULTIPLE LINEAR REGRESSION
PHYSIOGRAPHIC DIVISIONS
14 SELECT "BEST" MODELS
15 PERFORM SIMPLE CORRELATION ANALYSES BETWEEN WILDLIFE DENSITY AND HABITAT PARAMETERS
PHYSIOGRAPHIC DIVISIONS
16 HABITAT AS AN INDEX TO DENSITY OF WILDLIFE SPECIES
16 EVALUATION AND MANAGEMENT OF HABITAT FOR WILDLIFE SPECIES
17 DEVELOP MODEL FOR ENTIRE STUDY AREA
WEIGHT COMPONENT MODELS BY PERCENT LAND AREA
HABITAT PARAMETERS WITHIN "BEST" MODELS
DETERMINE DENSITY LEVELS TO DISCRIMINATE
17 DEVELOP DISCRIMINANT FUNCTION(S)
DISCRIMINANT ANALYSIS
18 TEST MODELS
PHYSIOGRAPHIC DIVISIONS
18 TEST DISCRIMINANT FUNCTION(S)
19 INVENTORY HABITAT PARAMETERS AND WILDLIFE SPECIES ON SAME TRANSECTS AT ESTABLISHED TIME INTERVAL
HABITAT PARAMETERS WITHIN "BEST" MODELS
HABITAT PARAMETERS WITHIN DISCRIMINANT FUNCTION
19 INVENTORY HABITAT PARAMETERS AND WILDLIFE SPECIES ON NEW TRANSECTS
MULTIPLE LINEAR REGRESSION
20 COMPARE PREDICTED DENSITIES AND CONFIDENCE LIMITS TO OBSERVED DENSITIES
20 PREDICT DENSITY LEVELS AND COMPARE TO OBSERVED LEVELS
B
C
D
B
C
D
21 DEVELOP "MARK SENSE" DATA COLLECTION FORMS AND GUIDELINES FOR CONDUCTING SURVEYS
PHYSIOGRAPHIC DIVISIONS
WILDLIFE DENSITY INDEX AND/OR HABITAT PARAMETERS
22 PREDICT ANNUAL FLUCTUATIONS IN WILDLIFE DENSITY
22 DETERMINE EFFECT OF HABITAT MODIFICATION ON WILDLIFE DENSITY OVER TIME
22 HABITAT EVALUATION AND MANAGEMENT USING DISCRIMINANT FUNCTION AND SIMPLE CORRELATION ANALYSES
23 INVENTORY HABITAT PARAMETERS ON SAME TRANSECTS DURING ESTABLISHED TIME INTERVAL
INCLUDE INVENTORY OF WILDLIFE SPECIES
HABITAT PARAMETERS WITHIN "BEST" MODELS
HABITAT PARAMETERS WITHIN DISCRIMINANT FUNCTION
23 INVENTORY HABITAT PARAMETERS IN TRANSECTS WITHIN AREA TO BE EVALUATED
MULTIPLE LINEAR REGRESSION
24 CALCULATE PREDICTED DENSITIES AND CONFIDENCE LIMITS
PHYSIOGRAPHIC DIVISIONS
PREDICTED DENSITY RELATIVE
PREDICTED DENSITY RELATIVE
24 PREDICT DENSITY LEVEL OF WILDLIFE SPECIES WITHIN AREA
DISCRIMINANT ANALYSIS
SIMPLE LINEAR REGRESSION
25 COMPARE PREDICTED DENSITIES OVER TIME AND ESTABLISH TREND
25 COMPARE TRENDS IN WILDLIFE DENSITY AND HABITAT OVER TIME
25 MANIPULATE HABITAT TO INCREASE HABITAT PARAMETERS POSITIVELY CORRELATED WITH WILDLIFE DENSITY

DISCUSSION

PAUL GEISSLER: I have two comments. First, you have an average of about eight times as many variables as transects in your initial analysis. Even counting the artificially increased sample sizes which resulted from using multiple surveys of transects as independent observations, you have an average of over twice as many variables as observations. In addition to the variables examined in your initial analysis, you also examined additional variables that were combinations of the original variables in the process of evaluating seven simplifications of habitat classifications. It does not matter that simplified habitat classifications were evaluated in separate computer runs, because these additional variables were still included in the search for a simple model with high predictive power.

Very high R^2's can be obtained from random numbers which have no predictive power whatsoever (figure 1D). This is due essentially to the repeated analyses on the same set of data by the stepwise procedure. When there are few observations relative to the number of variables, there is a tendency for the procedure to fit the random variations in the data as well as the underlying biological process. This results in prediction bias, the over-estimation of the model's predictive ability (R^2) based on the data used to construct the model as compared to the model's true predictive ability on other data (Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Ill. p.388). In other words, a very high R^2 indicating good predictive power may be obtained from the original set of data, but poor predictions and low R^2 result when the model is applied to another set of data.

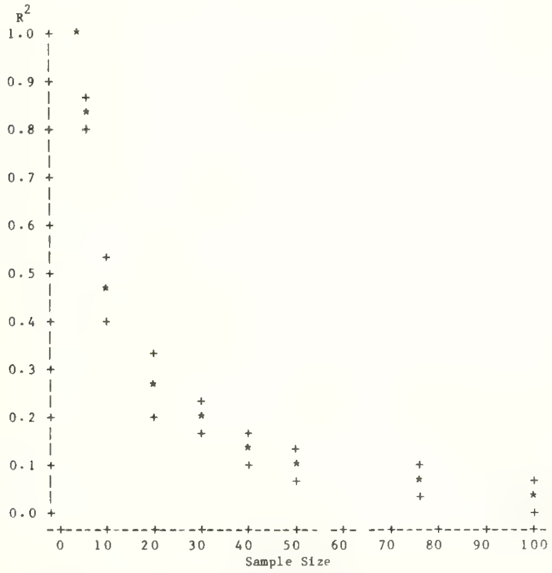


Figure 1D. Effect of sample size on R^2 in stepwise regression. One hundred sets of data were generated for each of the sample sizes of 3, 5, 10, 20, 30, 40, 50, 75, and 100 observations. Each observation consisted of a dependent variable and 10 independent variables generated as normally distributed random numbers. Each set of data was analyzed using the SAS Stepwise Procedure with default options (Barr et al., op. cit.) and the mean R^2 and the 95% confidence limits for the mean R^2 plotted as a function of sample size.

Using the Pineywoods as an example, you obtained a R^2 of 83.3% using a model with three variables selected from 98 variables present. There were nine transects in this area. Using independent normally distributed (0,1) random numbers in place in these 98 prediction variables and the response variable for nine independent transects, I calculated an R^2 of 100% 24 out of 25 times using the SAS Stepwise Procedure with default options (Barr, A.J. et al. 1979. SAS User's Guide. SAS Institute, Cary, N. C.). There are similar problems with the discriminant analysis unless there are substantially more independent observations than there are variables.

My second comment concerns the correlation among your call-count surveys. You indicate that audio count data for all of the surveys conducted on the 133 call-count transects were included instead of using transect means. This was done because differences in audio counts between surveys were significant. However, you note that "...inclusion of multiple surveys of individual transects artificially increased sample sizes within ecological areas, as surveys of the same transect were not statistically independent." A basic assumption in any regression analysis is that the error terms are uncorrelated (Neter and Wasserman, op. cit., p. 31). The test for a difference among surveys is not relevant to the determinations of the unit that constitutes an independent observation. That decision must be based on the lack of correlation among units. It is possible for there to be a perfect correlation (r=1) between the call-counts on multiple surveys of individual transects, and at the same time be significant differences among the surveys. What you need to demonstrate is that the survey results are uncorrelated, not that there is a significant difference among surveys. Analyzing the mean of the multiple surveys of a transect will result in uncorrelated observations and meet the assumptions required for regression analysis.

CHRIS GRUE: We were aware of the possibility of prediction bias throughout our study. The number of potential habitat types within our habitat classification was, unfortunately, nearly four times the number of call-count transects within Texas. We, however, considered the habitat classification to be suitable for classifying habitats from within a vehicle and an unbiased method of selecting the habitat variables to be included in the regression analyses; the classification scheme was developed prior to the collection of any field data. We believed the elimination of levels within the classification hierarchy was an objective means of simplifying the habitat classification and reducing the number of habitat variables therein. We also realized that, depending on the level within the habitat classification, only a fraction of the potential habitat variables might actually be observed along the call-count transects. With respect to the discriminant analyses, we decided to include only those habitat variables which entered the regression models.

Because the number of call-count transects was lower than the potential number of habitat variables, the decision of whether to conduct the regression analyses statewide or within ecological areas was difficult. Both approaches had apparent problems, statistical or biological. By conducting regression analyses statewide, the potential for prediction bias would be reduced. However, this approach appeared to suffer biologically. Habitat variables important to doves may not be expected to be the same within any two ecological areas due to differences in the abundance and distribution of habitat types. Analyses within ecological areas, though probably more valid biologically, increased the potential for prediction bias; we were restricted to sampling the existing call-count transects due to budget constraints. Since the two approaches appeared to have merit, we decided, apriori, to utilize both in the study.

To counter the possible effects of prediction bias in the regression analyses conducted within ecological areas, we included call-counts for all surveys as the dependent variable instead of transect means. Variability in call-counts between surveys was great and we believed its inclusion in the regression analyses would make it more difficult to obtain high multiple correlation coefficients. Because surveys of the same transect were not independent observations and their inclusion artificially increased sample size, we increased the significance level for entry of habitat variables into the models from the default value of $P<0.10$ (Barr et al., op. cit.) to $P<0.05$.

Multiple correlation coefficients for models from statewide and within-ecological-area analyses using call-counts for all surveys and transect means are presented in table 1D. Inclusion of call-counts for all surveys did make it more difficult to obtain high multiple correlation coefficients. Some prediction bias is undoubtedly present in the data, particularly models for ecological areas based on transect means. The amount of prediction bias present, however, cannot be assessed until the models are tested. We believe the amount of prediction bias present is

Table 1D. Correlations between mourning dove call-counts (all surveys conducted and transect means) and habitat variables (structural features and habitat types within the simplified habitat classification selected). Multiple correlation coefficients are expressed as percents. The number of habitat variables remaining in the models is given in parentheses.

Ecological area	No. habitat variables present	All surveys N	All surveys R^2	Mean of surveys N	Mean of surveys R^2
Pineywoods	54	32	81.3 (3)	9	100.0 (6)
Gulf Prairies and Marshes	40	18	28.3 (1)	6	100.0 (3)
Post Oak Savannah	49	33	87.5 (4)	9	100.0 (6)
Blackland Prairies	44	40	68.1 (3)	10	93.6 (3)
Cross Timbers and Prairies	46	62	71.5 (7)	17	27.0 (1)
South Texas Plains	43	70	74.7 (6)	18	86.1 (4)
Edwards Plateau	35	72	63.9 (7)	18	81.7 (4)
Rolling Plains	37	88	55.7 (4)	23	56.6 (2)
High Plains	34	52	63.9 (2)	14	89.5 (2)
Trans-Pecos	31	35	86.6 (3)	9	99.7 (4)
Texas	54	502	44.6(16)	133	38.2 (4)

substantially less than that suggested by your example. One would not expect to account for only 27% of the variation in call-counts given 17 transects and 46 habitat variables if prediction bias was severe. If one is willing to accept the results of our regression analyses in which the number of independent observations substantially exceeded the number of independent variables (e.g., 3X), then habitat variables still accounted for a significant portion of the variation in mourning dove call counts (ca. 40%) throughout Texas (table 1D). That regression models for ecological areas accounted for a greater proportion of the variation in call counts than the model for the State, however, appears to be reasonable biologically. Prediction bias in our discriminant analyses should not be great; the number of transects was two to seven times the number of habitat variables included.

BERNARD MORZUCH: What are the implications of using stepwise regression on the properties of the resulting parameter estimates in the regression analyses?

CHRIS GRUE: Compared to "all possible regression" procedures, predictive models generated by stepwise may not provide the best fit to a data set because a limited amount of stepping back is done. Models generated by either procedure may not include all independent variables significantly correlated with a dependent variable and individual regression coefficients may depend on the other parameters within a model. Models generated by either procedure are primarily restricted to predictive uses. Examination of correlation matrices may, therefore, prove useful in identifying all habitat parameters significantly correlated with wildlife density and in establishing guidelines for improving wildlife habitat.

Examples: Multivariate Analyses of Wildlife Habitats

INTERSPECIFIC DIFFERENCES IN NESTING HABITAT OF SYMPATRIC WOODPECKERS AND NUTHATCHES[1]

Martin G. Raphael[2]

Abstract.--To test for nest site differences among nine sympatric species of woodpeckers and nuthatches (hole excavators) in a Sierra Nevada mixed conifer forest, I located 306 active nests, measured forest stand characteristics on a 0.04 ha plot centered at each nest, measured characteristics of the nest tree, and used discriminant analysis to compare these nest site characteristics among bird species.

Three discriminant functions were considered. The first was associated most strongly with live tree basal area and canopy height. The second function was associated with nest tree species and nest tree height; the third was identified by nest tree diameter and top condition. Mean discriminant scores differed significantly among all but 3 of 36 possible pairs of species along at least one of these discriminant axes, indicating that nearly all bird species chose distinct nest sites. The distributions of discriminant scores along each axis, however, showed considerable overlap with nest sites of two sapsucker species being the most similar. Euclidian distance between mean scores was the most useful measure to characterize the similarity of species' nest sites.

Nest stand and nest tree variables contributed nearly equally to the discrimination between bird species. This analysis suggested that both of these sets of variables should be included in management prescriptions to provide habitat for cavity nesting birds.

Key words: Cavity nesting birds; cluster analysis; discriminant analysis; Euclidian distance; nuthatches; Sierra Nevada; woodpeckers.

INTRODUCTION

Cavity nesting birds comprise about 30% of the breeding bird species in western forests. Habitat management for these species requires, among other factors, the provision of adequate numbers of suitable nest sites, usually standing dead trees (Raphael and White 1978, Thomas et al. 1979). The question arises whether each species selects distinct nest sites or whether groups of species nest in trees with similar characteristics. Habitat management is simplified in the latter case since species with similar nest sites can be grouped into a reduced set of functional management units.

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[1] Paper presented at The use of multivariate statistics in the studies of wildlife habitat: a workshop, April 23-25 1980, Burlington, Vt.

[2] Staff Research Associate, Department of Forestry and Resource Management, University of California, Berkeley, CA 94720.

The purpose of this study was to determine whether the nest sites of each species in a group of sympatric primary cavity nesters were distinct or whether one can identify subsets of species using nest sites with similar characteristics. To do so, I performed a one-way multivariate analysis of variance using discriminant analysis, followed by an examination of the relative separation of all possible species-pairs. The basic advantages of using discriminant analysis instead of a series of single-variable comparisons among all species are that it: a) accounts for correlations among the variables used in the analysis, and b) allows more rigorous control over the experiment-wise (type I) error rate.

Primary cavity nesters excavate their own cavities and to do so they must choose the appropriate substrate for the nest. Secondary cavity nesters, on the other hand, choose appropriate cavities, usually abandoned woodpecker holes (Raphael 1980). I limited the analysis to primary cavity nesters because these species select trees; the secondary cavity nesters choose cavities and this confounds an analysis of tree characteristics.

METHODS

Study Area

Field studies were conducted at the University of California Sagehen Creek Field Station, located on the east side of the Sierra Nevada, 13 km north and 6 km west of Truckee, California. Elevations in the 39 km² Sagehen Creek drainage vary from 1800 m to 2300 m. The drainage is dominated by a mix of Jeffrey pine (Pinus jeffreyi) and white fir (Abies concolor) and by brushfields or conifer plantations on the site of the 1960 Donner Ridge fire which burned the eastern quarter of the basin. Meadows, lodgepole pine (Pinus murryana), and aspen (Populus tremuloides) occur in mesic sites, and red fir (Abies magnifica) and mountain hemlock (Tsuga mertensiana) dominate at higher elevations.

Searches for active nests were conducted throughout the Sagehen Creek basin from 1976 to 1979. Active nests were confirmed by observing adults entering a cavity to incubate eggs or feed young and by the sounds of young calling from a nest.

Measurement of Nest Site Characteristics

I measured seven variables describing the characteristics of the stand within a 0.04 ha circular plot centered at each nest. These were 1) habitat (classified as burned or unburned); 2) canopy height (maximum height, measured using a relaskop); 3) basal area of live trees (computed from diameters of all live trees > 8 cm DBH excluding nest tree); 4) shrubcover (estimated percent canopy cover of all woody perennials including trees ≤ 8 cm DBH); and 5-7) density of small (< 23 cm DBH), medium (23-38 cm), and large (> 38 cm) snags.

Characteristics recorded for each nest tree included: 1) tree condition (live or dead); 2) diameter (DBH, measured with a diameter tape); 3) height (measured with a relaskop); 4) bark cover (estimated percent of stem covered by bark); 5) top condition (broken or intact); 6) twig condition (most foliage-bearing twigs present or most broken); 7) tree species (Jeffrey pine, lodgepole pine, red fir, white fir, or other).

All binary variables were coded as 0 or 1 for subsequent analyses. Tree species was converted to four dummy binary variables. If the tree was a given species it was assigned a value of 1; otherwise, it was assigned a 0. The fifth group, other, was left out of the analysis to avoid redundancy. In total, then, 17 variables were included in the analysis.

Statistical Analyses

A linear discriminant analysis was performed on all 17 variables (percentages analyzed using an arcsine transformation) using the SPSS (version 8.0) package (Nie et al. 1975). The null hypothesis was that nest sites of all species are equal, that is, the mean discriminant scores do not differ between members of any possible pair of species.

The maximum number of functions derived in a multi-group discriminant analysis is either one less than the number of groups (in this case, bird species) or equal to the number of variables entered into the analysis, whichever is smaller. The first function derived explains the greatest proportion of the total variance, and each additional function explains successively less. There are two approaches in deciding how many of the possible functions to consider. First, one can test the statistical significance of each function by comparing the additional variance explained by that function to an expected value (Klecka 1975, Morrison 1976). Alternatively, one can arbitrarily define a minimum proportion of explained variance and accept only those functions that explain more than that minimum. In this study, I chose the latter approach and considered only those functions explaining 5% or more of the total variance. This alternative allows more powerful planned comparisons of mean discriminant scores among the groups as opposed to post-hoc comparisons which would have been necessary had I used the former approach.

To interpret the biological meaning of each discriminant function, I computed the correlation of each variable with the discriminant score derived for each function (structure matrix). Variables with the highest correlations were used to interpret functions. Some researchers (e.g., Klecka 1975:443) prefer to use the standardized discriminant function coefficients (pattern matrix) to interpret functions, but these coefficients can be highly unstable.[3]

I used a t-test to compare mean discriminant scores of each pair of species along each of the discriminant axes accepted for analysis. Given S species, there are [S(S-1)]/2 possible pairwise comparisons on each axis. To control the total type I error rate at ≤ 0.05 for all comparisons on each axis, I used Dunn's (1961) procedure for multiple planned comparisons. Assuming equal variance in discriminant scores, the formula used for each pairwise test comparing species i and j on the kth discriminant axis is simply:

$t_k = (\bar{d}_{ik} - \bar{d}_{jk}) \;/\; (1/n_i + 1/n_j)^{1/2}$ where $\bar{d}$ is the mean discriminant score and n is the sample size for each species. Values of t were compared to values tabled by Dunn (1961) to accept or reject the null hypothesis of no difference between mean scores at the 0.05 significance level.

The value of t is dependent on sample size as well as the magnitude of the difference between the discriminant scores. Given the same value of $(\bar{d}_{ik} - \bar{d}_{jk})$, a comparison involving two species with large sample sizes may be statistically significant while a comparison of species with smaller sample sizes may not be. Values of t may also be affected by unequal variance in scores among species. To reduce this dependency on sample size and to account for the possibility of unequal variance, I divided each discriminant axis into equal segments, computed the frequency of discriminant scores for each species in each segment, and then computed the similarity of these frequency distributions along each axis using a measure of niche overlap given by Colwell and Futuyma (1971:573, equation 23). Since each discriminant axis is independent, I multiplied the overlap values for each species-pair on each axis to derive an index of total overlap on all axes (May 1975). Cluster analysis (UPGMA, Sneath and Sokal 1973) was used to reveal possible groups of species using nests with similar characteristics based on these total overlap values.

For comparison, I also computed the Euclidian distance (D_{ij}) between each pair of species i and j in discriminant space, using the formula:

$D_{ij} = [\sum_k (\bar{d}_{ik} - \bar{d}_{jk})^2]^{1/2}$, where $\bar{d}_{ik}$ is the value of the mean discriminant score on the kth axis for the ith species, and d_{jk} is the value for the jth species on the same axis (D_{ij} is equivalent to the square root of the Mahalanobis distance statistic). Like the overlap values described above, these Euclidian distances are less affected by sample size than the t-test.

To compare the relative importance of the nest tree and nest stand variables as discriminators between nest sites of the species, I performed three additional discriminant analyses. For the first analysis, I included only the seven nest stand variables and computed the proportion of the total variance explained by all functions (sum of squares between groups divided by the total sum of squares). Second, I used a stepwise analysis to determine the best seven of the ten nest tree variables and calculated the proportion of the total variance explained by these seven variables. Third, I used a stepwise analysis including both the nest tree and nest stand variables and calculated the proportion of the total variance explained by the first seven variables entered of either type. I then compared these values of explained variance from each analysis to assess the relative importance of the tree and stand variables.

RESULTS AND DISCUSSION

Interpretation of Functions

I located a total of 306 nests of 9 excavator species (table 1). These species formed nine groups resulting in eight discriminant functions which explained 83% of the total variance in nest site characteristics (fig. 1). Each of functions 4 through 8 explained less than 5% of the variance not accounted for by previous functions and was not considered in subsequent analyses. The first three functions explained 55%, 11%, and 7%, respectively, totaling 75% of the variance.

The first function was correlated most highly with canopy height, live tree basal area, and burned vs. unburned habitat (table 2). This function clearly was associated with nest stand variables and separates species nesting in unburned forest stands (red-breasted nuthatch and sapsuckers) from those nesting in burned stands (pygmy nuthatch, and Lewis and white-headed woodpeckers) (fig. 2A). The three remaining species nest in both burned and unburned habitats and their mean discriminant scores were located at intermediate locations on the first discriminant axis (fig. 2A).

The second discriminant function was most correlated with nest tree variables, particularly species (the two fir categories) and tree size (height and diameter) (table 2). Species nesting in red fir and smaller size trees had the lowest discriminant scores (black-backed and white-headed woodpeckers) and species nesting in larger size, white fir trees had the highest scores (Lewis

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[3] Personal communication with L.A. Marascuilo, statistics Professor, Department of Education, University of California, Berkeley.

Table 1. Bird species (hole excavators) nesting in the Sagehen Creek study area.

Bird species	Code	Sample size
Common flicker (*Colaptes auratus*)	CF	68
Lewis woodpecker (*Asyndesmus lewis*)	LW	37
Red-breasted sapsucker (*Sphyrapicus ruber daggetti*)	RS	50
Williamson sapsucker (*Sphyrapicus thyroideus*)	WS	50
Hairy woodpecker (*Dendrocopos villosus*)	HW	23
White-headed woodpecker (*Dendrocopos albolarvatus*)	WW	12
Black-backed-three-toed woodpecker (*Picoides arcticus*)	BW	8
Red-breasted nuthatch (*Sitta canadensis*)	RN	30
Pygmy nuthatch (*Sitta pygmaea*)	PN	28
TOTAL		306

woodpecker and red-breasted-sapsucker) (fig. 2B). The mean scores of the other five species differed very little on this axis.

The third discriminant function was also associated with variables describing the nest tree (table 2) and it separated the white-headed, hairy, and black-backed woodpeckers from the remaining species (fig. 2C). The white-headed woodpecker nests in large diameter, broken-topped trees while the black-backed and hairy woodpeckers nest in smaller diameter, intact-topped trees. As with the second function, the remaining species have very similar mean scores on this axis.

Pairwise Comparisons

Results of the 36 t-tests comparing mean discriminant scores among all possible pairs of species on each discriminant axis are summarized in figure 3. The null hypothesis of no difference between mean scores was rejected on at least one axis for all but three comparisons (RN vs. WS, BW vs. HW, WS vs. RS). These results might be used to suggest that the black-backed and hairy woodpeckers could be grouped for management purposes because their nest site characteristics were statistically indistinguishable. Similarly, the two sapsuckers could also be grouped. The pygmy nuthatch is more problematic since its nest sites are similar to those of the Williamson sapsucker but not to those of the red-breasted sapsucker; it might be better, therefore, not to group pygmy nuthatches with either species.

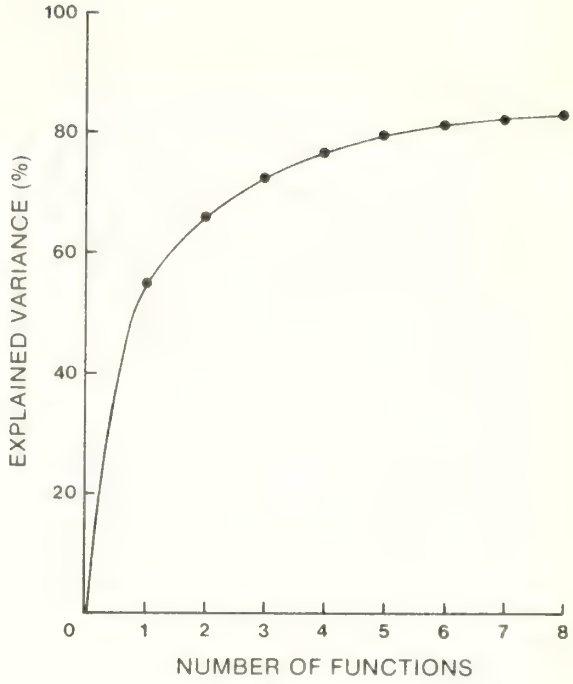

Figure 1. Cumulative explained variance (% of total variance) in relation to the number of discriminant functions considered.

Because all discriminant axes are orthogonal (independent), a significant difference between two species' centroids on any one axis is sufficient to conclude that the two species use statistically distinct nest sites. Given that the null hypothesis is true and that the probability of at least one significant difference on each axis is 0.05, the probability of no difference on any axis is $(1.00 - 0.05)^3 = 0.86$. Thus, for 36 comparisons one could expect approximately 36(0.86) = 31 to be nonsignificant. Clearly, since only three comparisons were actually nonsignificant, the null hypothesis is not true. It is unclear, however, whether the lack of a significant difference among these three pairs reflects their inherent ecological similarity or a chance event.

Interpretation of these pairwise comparisons is further complicated by the fact that the comparisons along any one axis are not independent. When significant differences do occur among comparisons of this type, they tend to occur in "bunches" (Lindman 1974:82). Therefore,

Table 2. Pooled within-groups correlations between discriminant functions and discriminating variables.

Variable	Correlation with Discriminant Function: 1	2	3
Nest Stand Variables			
Canopy height	0.83	0.12	-0.03
Live tree basal area	0.70	0.07	-0.16
Burned or unburned	-0.59	0.10	-0.03
Shrub cover	-0.26	-0.19	0.12
Snags < 23 cm DBH	0.02	-0.18	0.05
Snags 23-38 cm DBH	-0.14	-0.06	0.05
Snags > 38 cm DBH	-0.15	0.01	-0.07
Nest Tree Variables			
Height	0.51	0.43	0.20
Diameter	0.31	0.32	-0.53
Foliage-bearing twigs	0.52	0.19	0.14
Bark cover	0.29	0.17	-0.27
Top condition	0.23	-0.17	0.38
Jeffrey pine	-0.26	0.04	-0.21
Lodgepole pine	0.21	-0.06	0.31
White fir	-0.08	0.28	0.00
Red fir	0.08	-0.47	-0.15
Tree condition	-0.44	-0.10	0.01

one cannot predict, a priori, the expected number of significant differences on one, two, or three discriminant axes. For these reasons, pairwise comparisons of species' mean discriminant scores appear to have limited utility in assessing habitat similarity among the species. Two other measures, involving overlap of score distributions and distance between mean scores, seem better suited for such a purpose.

Overlap of Discriminant Scores

The range and standard deviation of discriminant scores on the discriminant axes show considerable overlap among species (fig. 2). Two species may have statistically different mean scores but their score distributions could overlap to such an extent that they might justifiably be grouped for management purposes. To examine such a possibility I computed overlaps between all pairs of species on each of the three discriminant axes and multiplied the three overlap values for each species-pair to derive an index of nest site similarity (table 3). The greatest overlap values are found between the two sapsuckers (0.42) and between the common flicker and pygmy nuthatch (0.40).

I used a cluster analysis based on this similarity matrix (overlap values) to produce a dendrogram (fig. 4) revealing patterns of nest site similarity among the bird species. At the 0.4 level, two groups are recognized, one composed of the two sapsuckers and another containing the pygmy nuthatch and common flicker. At the 0.2 level, the Lewis woodpecker links with the flicker-pygmy group and the red-breasted nuthatch joins the sapsucker group. At this level of similarity, these groups can be indentified as burn and unburned specialists, respectively. The remaining species link at successively lower overlap values. These results suggest that nest sites of the two sapsuckers may be similar enough to permit their management in common and, likewise, those of the pygmy nuthatch and common flicker. The pairwise t-test also identified the sapsucker group, but the t-tests indicated the hairy and black-backed woodpeckers as a second possible group rather than the nuthatch and flicker.

Euclidian Distance

Another measure of overall nest site similarity is the Euclidian distance between species' mean discriminant scores. These values (table 3) measure the separation of the species in discriminant space, and may be less affected by sample size than the overlap values. For example, the overlap of the black-backed woodpecker with the other species ranges from 0.01 to 0.02 (table 3). These values are lower than the average of any other species, probably reflecting the small sample size of black-backed nests ($n = 8$). In contrast, the Euclidian distances between black-backed nests and those of the other species range from 1.30 to 3.24 and these values are spread throughout the range exhibited by the other species-pairs.

Euclidian distances, however, do not directly convey any information about the dispersion of each species about its centroid. The overlap values do convey such information, since it is precisely the relative patterns of dispersion of any two species that define their overlap. But, a linear regression of discriminant score overlap with Euclidian distance between mean scores in three-dimensional discriminant space showed that the two measures were highly correlated ($r = -0.89$, $P < 0.001$, excluding the black-backed woodpecker). Thus, overlap can be predicted from Euclidian distance. Given this relationship, and

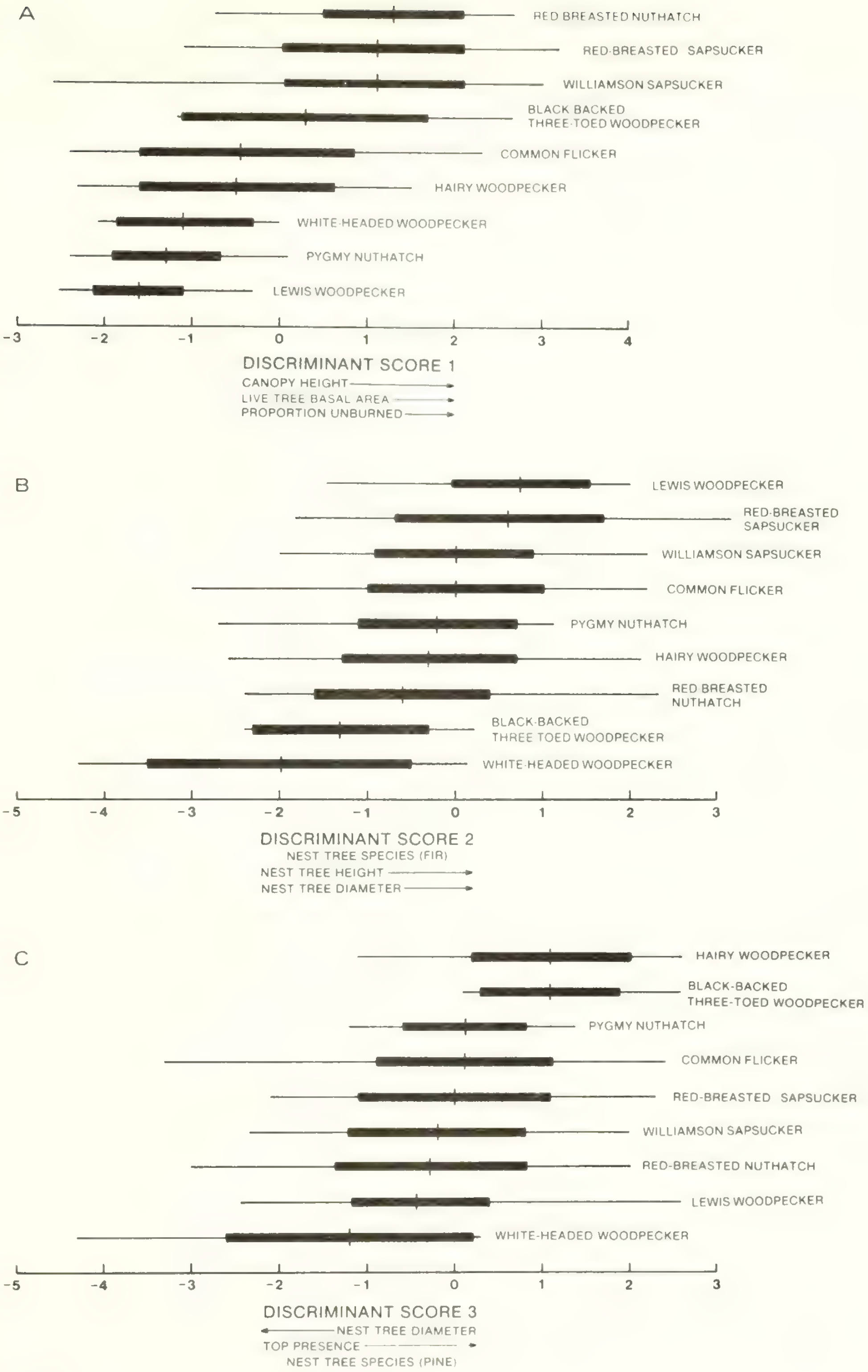

Figure 2. Mean (vertical lines), standard deviation (heavy bars), and range (horizontal lines) of discriminant scores of each bird species on the first (A), second (B), and third (C) discriminant functions. Arrows indicate direction of increased values of variables most highly correlated with the discriminant scores on each function.

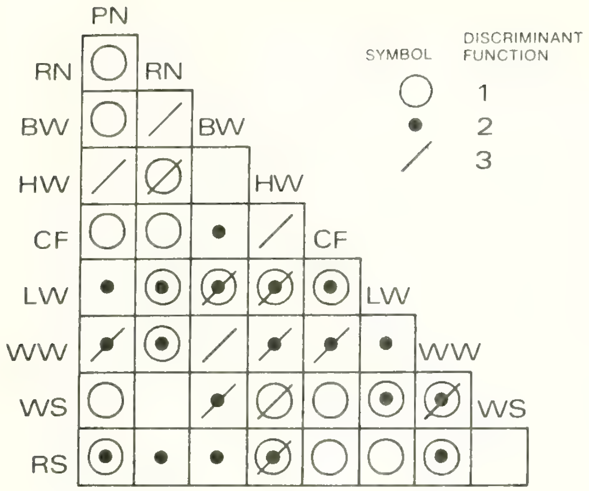

Figure 3. Results of t-tests comparing mean discriminant scores among all possible pairs of species on each function. Symbols denote significant differences (see text). Species codes are given in table 1.

the observation that Euclidian distances are apparently less dependent on sample size than the t-tests or overlap values, I recommend using Euclidian distance as a measure of similarity when sample sizes of some groups are small. When sample sizes are large, the overlap value is preferred since it is directly interpretable as a measure of shared discriminant score distribution.

Relative Importance of Stand and Tree Variables

Figure 3 shows that eight pairs of species differ only on the basis of stand characteristics (significant differences occur only on the first discriminant axis). These species nest in similar trees located within otherwise different stands. In contrast, 13 species-pairs nest in trees with significantly different characteristics (significant differences occur only on functions 2 and/or 3). They nest in differing trees located in otherwise similar stands. The remaining 12 pairs of species nest in both different trees and stands.

Three additional discriminant analyses, each using seven variables, were used to assess the relative discriminating power of the tree and

Table 3. Relative similarity of excavator nest sites. Values to right of diagonals are the overlaps of species' discriminant score distributions (larger values indicate more similar nest sites). Values to left of diagonals are Euclidean distances between species' mean discriminant scores in three-dimensional discriminant space (larger values indicate less similar nest sites).

Bird species[1]	PN	RN	BW	HW	CF	LW	WW	WS	RS
PN	----	0.02	0.03	0.19	0.40	0.22	0.11	0.05	0.09
RN	2.72	----	0.02	0.06	0.17	0.01	0.01	0.24	0.21
BW	2.21	1.90	----	0.02	0.02	0.01	0.02	0.01	0.02
HW	1.30	2.36	1.33	----	0.22	0.04	0.02	0.10	0.13
CF	0.91	1.93	1.85	1.08	----	0.26	0.09	0.28	0.32
LW	1.15	3.24	3.24	2.20	1.48	----	0.01	0.02	0.04
WW	2.23	2.91	2.75	2.93	2.48	2.87	----	0.02	0.02
WS	2.47	0.69	2.09	2.15	1.59	2.82	3.12	----	0.42
RS	2.59	1.25	2.40	2.21	1.68	2.79	3.59	0.60	----

[1] See table 1 for bird species codes.

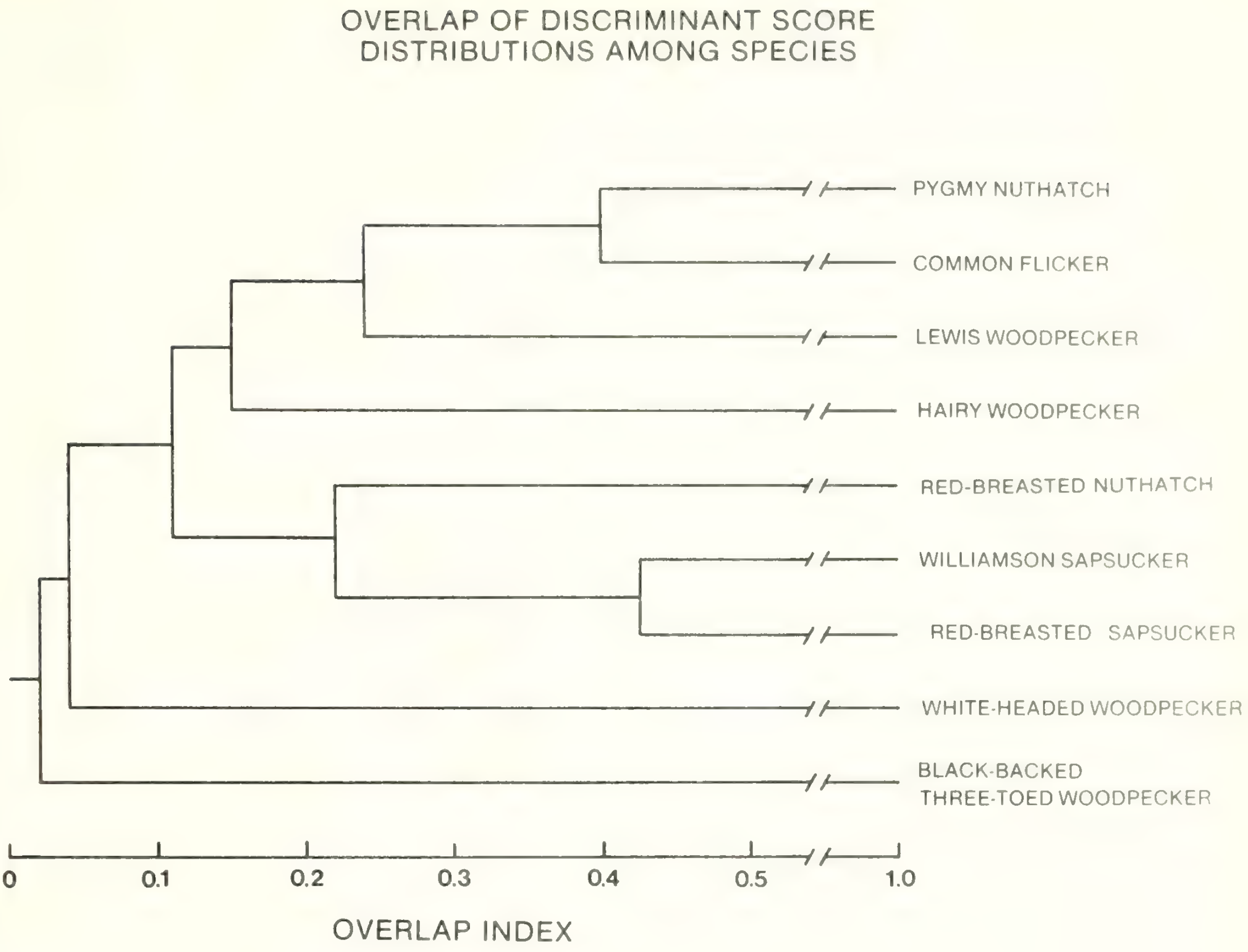

Figure 4. Dendrogram showing similarity of nest sites of bird species based on cluster analysis using overlap of discriminant score distributions along three discriminant axes. Larger index values indicate more similar nest sites.

stand variables (see methods). When only the seven stand variables were included in the analysis, the variance explained by the set of discriminant functions was 60% of the total variance in the system. The variance explained using only the best seven nest tree variables (lodgepole pine, white fir, and foliage bearing twigs were excluded) is slightly higher, 63%. Finally, the optimum set of both nest and stand variables (canopy height, tree height, tree diameter, red fir, live tree basal area, top condition, and tree condition listed in order of entry in stepwise analysis) explained 74%. While the nest tree variables are slightly better than the stand variables as discriminators between species' nest sites, it is apparent that both types of variables should be included to adequately characterize nest sites. Consideration of both types resulted in a substantially greater separation of species' nest sites.

CONCLUSION

Discriminant analysis is a useful method for quantifying the similarity of habitat characteristics among wildlife species. It offers several options including planned or post-hoc comparisons of mean scores, analysis of score distributions in discriminant space, and measures of the separation of species such as Euclidian distance. Of these options, Euclidian distance appears to have the greatest generality since it is affected less by variation in sample size among the species analyzed.

Using discriminant analysis to compare the characteristics of the nest sites of nine sympatric primary cavity nesting bird species, I demonstrated that both nest tree and nest stand characteristics should be included in the suite of variables used by managers to prescribe management practices to provide the habitat requirements of these species. Five species used distinct nest sites and require unique management prescriptions, but the four other species can be combined for management purposes into two groups, each containing pairs of species using very similar nest sites.

As a final note, researchers (and managers) must recognize that interspecific comparisons of habitat characteristics are not sufficient to define the most important variables involved in habitat selection. For example, nests of all species considered in this study were surrounded by a relatively large number of snags greater than 23 cm DBH. But because the magnitude of this variable does not vary significantly among species, snag density is not a good discriminator between species' nest sites. When snag density is compared between a species' nest sites and a set of random plots, however, it becomes one of the best discriminators (Raphael 1980). Thus, variables important in habitat selection should be identified through a series of single species analyses comparing use and availability of habitat components rather than by comparing habitat characteristics among all species of interest.

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DISCUSSION

DONALD McCRIMMON: Please reiterate the method used to interpret discriminant axes.

MARTIN RAPHAEL: I calculated the correlations between each original variable and the discriminant score for each function (structure matrix) and interpreted the functions by considering the most highly correlated variables.

PAUL GEISSLER: I think it would be more appropriate to use a multivariate analysis of variance (MANOVA) to test for differences among species, possibly with orthorgonal contrasts based on taxonomic relationships. The criteria in MANOVA are functions of the eigenvalues associated with the eigenvectors which define the discriminant functions. It has been suggested that plots of the treatment means in the space of the discrimination functions be used to interpret MANOVA results.

MARTIN RAPHAEL: I believe that a one-way MANOVA and the multi-group discriminant analysis are the same procedure. I would not want to limit the contrasts to taxonomic relations. For example, I found that the common flicker and pygmy nuthatch--two very distantly related species--were highly similar in nest site selection.

KEN WILLIAMS: Did you check for covariance hetergeneity? Without this characteristic it is difficult to test your stated hypothesis. Also, it assures some degree of overlap distortion as displayed by the discriminant functions.

MARTIN RAPHAEL: I did test for variance/covariance heterogeneity, and the variance/covariance matrices were not equal. I could find no method to assess the consequences of the failure to meet this assumption, and decided to proceed with the analysis since some authors state that the procedure is robust against such a failure. My understanding is that this failure has more severe implications on the interpretation of discriminant coefficients. It is quite possible that distortions occurred in the pattern of overlaps among the species; I would ask how severe such distortion might be: are they so severe that the results are wrong? No one, as yet, can answer the latter question.

LESLIE MARCUS: I suggest that you plot points or bivariate ellipse projections into canonical variate space, to see how covariance-structure looked in bivariate space. You could use the term "Mahalanobis distance" rather than "Euclidean distance in discriminant space"--as one always knows what it means.

MARTIN RAPHAEL: To answer the first point, I cannot visualize the advantage of plotting such projections since any distortions caused by the covariance structure would still affect the bivariate axes. I would like to know more about such a technique if it really would allow an evaluation of distortions. On the second point, I suppose it is a matter of personal taste since the two measures are so closely related. It would be useful to agree on the use of either measure to facilitate communications.

ROBUST CANONICAL CORRELATION OF SAGE GROUSE HABITAT[1]

Mark S. Boyce[2]

Abstract.--The distribution patterns of sage grouse (Centrocercus urophasianus Bonaparte) were studied on Atlantic Richfield Company's Coal Creek coal surface mine site in northeastern Wyoming. Fecal droppings were periodically removed from randomly located belt transects within a 36 km^2 study area. Using multiple regression and canonical correlation the seasonal distribution of droppings was related to several habitat variables which were hypothesized to be important to sage grouse. By canonical correlation, approximately 90% of the variance in a fecal count variate can be attributed to a habitat variate. The correlations between each variate and the original variables were found to be very stable when habitat variables were rotated. Similarly, the robustness of the loadings was confirmed by systematically eliminating cases (transects) from the analysis. Although canonical correlation provides little insight here over that obtained from multiple regression analysis, it does provide a succinct summary of a large and complex set of interrelationships among variables.

Key words: Canonical correlation; habitat; mine reclamation; multiple regression; patchiness; sage grouse; Wyoming.

INTRODUCTION

Applications of canonical correlation in ecology are relatively uncommon (Smith 1980). This may be due in part to unstable results or difficult interpretation (Gauch and Wentworth 1976, Johnston[3]). These problems are often attributable to assumption violations in the data, e.g., variables which are not normally distributed (Harris 1975), multicollinearity among variables (Cohen et al. 1979), or nonlinearity (Gauch and Wentworth 1976). However, if these assumptions can be approximated, the potential is great for application of canonical correlation in habitat studies. Canonical correlation searches for the maximum correlation between linear combinations of two sets of variables; for example, one set of variables may consist of measures of organism distribution and/or abundance, and another set may consist of variables characterizing habitat.

In this paper I describe an application of canonical correlation to an analysis of sage grouse habitat. One set of variables consists of the number of sage grouse fecal droppings deposited in different seasons, whereas the second set of variables consists of selected habitat variables which were hypothesized to be important factors influencing sage grouse distribution. Correlations between the original variables and the derived distribution and habitat variates were found to be robust (contra Cohen et al. 1979), even though the sample size was relatively small

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

[2] Assistant Professor, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071.

[3] Personal communication with R.F. Johnston, Professor, University of Kansas.

(n = 20). I attribute the robustness of this application of canonical correlation to thorough screening for nonlinearity and normality followed by transformation or elimination of variables before conducting the analysis.

METHODS AND MATERIALS

The study area was a 36 km² coal lease (T46N, R70W) in Campbell County, Wyoming which is scheduled for development as a surface mine. An objective of this research was to characterize the habitat components which are most important to sage grouse and to develop guidelines for reclamation of mined lands for sage grouse.

Sage grouse fecal droppings are easily identified and may last for up to 3 years before deteriorating. A sampling scheme was designed to assess seasonal distribution of sage grouse by periodically checking permanent belt transects for fresh droppings, and removing all droppings deposited since transects were last searched. Twenty 2 m x 1000 m belt transects were randomly located on the study area, and checked at irregular intervals.

An independent consulting team was employed to map and characterize all vegetation types on the study area (Keammerer and Keammerer 1975). In addition, detailed data were collected on the composition of sagebrush density, height and cover along each transect by employing systematic point-quarter procedures (Seber 1973).

The total number of fecal pellets found during a particular season was summed over the three years of our study, yielding three seasonal distribution variables, i.e., number of droppings found in 1) winter, 2) spring, and 3) summer through early fall. Habitat use patterns are known to be very similar in summer and early fall in non-migratory sage grouse populations (Patterson 1952). Habitat and distribution variables employed in this analysis are listed in table 1.

Table 1. Reduced set of variables and appropriate transformations for variables used in this analysis.

Distribution variables

TOTAL = $\log_{10}$ (total droppings found on each transect over 3 years, plus 1.0).

SUMMER-FALL = $\log_{10}$ (sum over 3 years of all droppings which accumulated between June and October, plus 1.0).

WINTER = $\log_{10}$ (droppings accumulated during winter months, plus 1.0).

SPRING = $\log_{10}$ (sum over 2 years of droppings accumulated during spring months through mid-May, plus 1.0).

DIST = fecal droppings canonical variate.

Habitat variables

LEK = distance between the nearest sage grouse strutting ground (lek) and the closest point on each belt transect in km.

FORBS = summed area within each belt transect within forb-producing habitats, including riparian areas, in m².

DIV = habitat diversity = $-\Sigma p_i \log p_i$ where p_i is the proportion of the ith habitat type within each belt transect.

PATCH = patchiness index equal to the number of times the belt transect crosses from one habitat type to another, plus 1.0.

SPRAY = $\log_{10}$ (area within belt transect of big sagebrush habitat which had been sprayed with 2,4-D, plus 1.0).

COVER = average sagebrush cover along transect estimated with 21 point-quarter measurements (Seber 1973).

VACOV = standard deviation of COVER.

DENS = average density of sagebrush plants per m² estimated from 21 point-quarter measurements (Seber 1973).

VADEN = standard deviation of DENS.

SAGE = area within belt transect of big sagebrush habitat type in m².

HABITAT = canonical variate comprised of habitat variables.

RESULTS

An average of 360 droppings was found on each transect. All variables were screened for skewness and kurtosis, and transformations conducted where appropriate. Seven variables were either eliminated or combined with other variables because their distribution contained an excessive proportion of zeros. Next, because of the sensitivity of canonical correlation to non-linearity (Gauch and Wentworth 1976), bivariate plots were constructed between the distribution variables and each habitat variable. When nonlinear patterns appeared, the respective habitat variable was eliminated from the analysis. For example, the total droppings vs. the area within each belt transect in the big sagebrush habitat type appears nonlinear (fig. 1). The availability of at least some big sagebrush is essential, and transects with no big sagebrush have no sage grouse utilization. However, large homogeneous stands of sagebrush tend to have low forb availability and are not preferred habitat. Therefore, SAGE was eliminated from further analysis.

A multiple regression analysis was conducted using each distribution variable as a dependent variable. This permitted explicit hypothesis testing regarding the importance of various habitat variables. Several interesting patterns emerge; for example, habitat patchiness and the proportion of forb-producing habitats were both positively correlated with the number of droppings found on each belt transect (fig. 2). Different habitat variables are important at different times of the year due to the seasonal changes in food habits and behavior of the grouse. A few of the more interesting multiple regression models are summarized in table 2.

In an attempt to summarize the complex interrelationships between the seasonal distribution patterns and habitat, I conducted a canonical correlation analysis of the "distribution" set of variables and a selected set of habitat variables. Due to the small sample size (n = 20), I began with a small number of variables: three distribution variables, and three of the most important habitat variables. As presented in figure 3A, a habitat variate accounts for almost 90% of the variance in a distribution variate and the relationship is highly significant (P << 0.001). Furthermore the correlations between the first pair of canonical variates and the original variables are all intuitively satisfying and parallel the results of multiple regression. The second canonical correlation was not statistically significant (P < 0.05), and loadings of the second pair of variates were not readily interpretable.

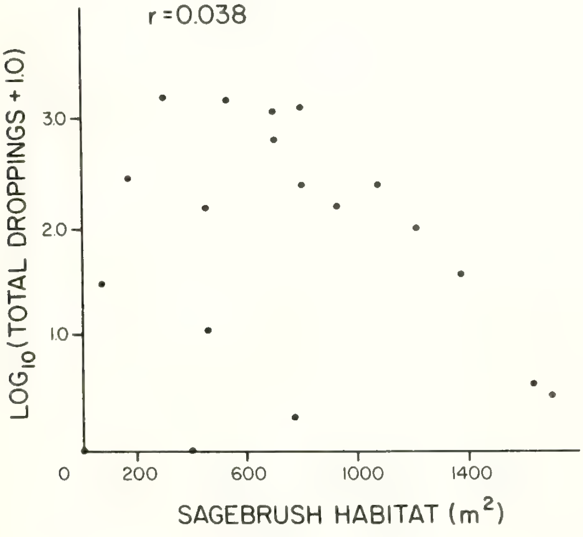

Figure 1. Total droppings over three years plotted as a function of the area within each belt transect in the big sagebrush habitat type.

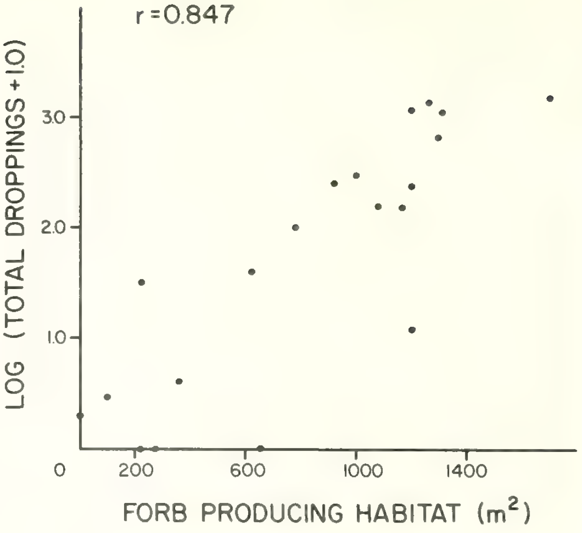

Figure 2. Total droppings over there years as a function of the area within each belt transect in forb-producing habitat types.

Since the 3 x 3 analysis worked so well, the number of habitat variables in the model was increased to assess whether a better synopsis of the interrelationships between habitat and distribution could be achieved. The analysis was attempted with five habitat variables (fig. 3B) and then with nine habitat variables (fig. 3C). The high stability of the loadings was impressive, i.e., the correlations between the first pair of canonical variates and the original variables remained relatively constant as additional habitat variables were added to the analysis. Even more exciting, however, the loadings were intuitively reasonable, and provided an exceptionally good representation of the interrelationships between variables which I had discovered through a tedious and detailed multiple regression analysis. All distribution variables loaded positively into a distribution variate, thus clearly the distribution variate reflected intensity of use by sage grouse. Correlations between original variables and the habitat variate all reflected quality of sage grouse habitat, i.e., variables which were positively correlated tend to be preferred habitat components and variables which were inversely correlated with the habitat variate were usually inversely correlated with the number of droppings found on transects at various times of year.

To test the robustness of the canonical correlations and variable loadings, the 3 x 9 analysis was rerun 20 times, each time leaving out one case (transect) from the analysis (similar to

Table 2. A sample of multiple regression models with droppings counts as dependent variables and habitat attributes as independent variables. All models listed account for a significant proportion of the variance in dependent variables ($P < 0.05$).

SPRING = 2.674 - 0.452(LEK) - 0.056(SPRAY)	R = 0.780
SPRING = 1.603 - 0.359(LEK) + 0.002(FORBS)	R = 0.841
SPRING = 0.002(FORBS) + 10.6(COVER) - 0.413	R = 0.818
SPRING = 3.367(DIV) + 13.0(COVER) - 0.686	R = 0.745
SPRING = 0.936 - 0.251(LEK) + 0.002(FORBS) + 5.8(COVER)	R = 0.864
SPRING = 2.706 - 0.481(LEK)	R = 0.779
SPRING = 0.003(FORBS) - 0.163	R = 0.680
SPRING = 0.313 + 14.56(COVER)	R = 0.671
SUMMER-FALL = 0.826 + 0.002(FORBS) - 0.414(SPRAY)	R = 0.896
SUMMER-FALL = 0.467 + 0.116(PATCH) + 0.002(FORBS) - 0.416(SPRAY)	R = 0.912
SUMMER-FALL = 0.664 + 2.3(DIV) - 0.265(LEK) + 0.002(FORBS)	R = 0.879
SUMMER-FALL = 0.812 + 2.28(DIV) - 0.133(LEK) + 0.001(FORBS) - 0.325(SPRAY)	R = 0.923
SUMMER-FALL = 0.994 + 3.54(DIV) - 0.165(LEK) - 0.371(SPRAY)	R = 0.910
SUMMER-FALL = 0.623 + 3.56(DIV) - 0.528(SPRAY)	R = 0.887
SUMMER-FALL = 0.995 - 0.241(LEK) + 0.002(FORBS)	R = 0.861
SUMMER-FALL = 1.88 - 0.624(SPRAY)	R = 0.810
SUMMER-FALL = 0.003(FORBS) - 0.191	R = 0.782
WINTER = 1.747 - 2.5(DIV) + 0.002(FORBS) - 0.423(SPRAY) - 0.238(VADEN)	R = 0.680
WINTER = 1.234 + 0.001(FORBS) - 0.42(SPRAY) - 0.216(VADEN)	R = 0.649
WINTER = 1.935 - 0.555(SPRAY) - 0.207(VADEN)	R = 0.583
WINTER = 1.184 - 0.314(SPRAY)	R = 0.437
TOTAL = 1.42 + 4.798(DIV) - 0.374(LEK)	R = 0.823
TOTAL = 0.718 + 0.003(FORBS) - 0.26(SPRAY)	R = 0.881
TOTAL = 2.415 - 0.598(SPRAY)	R = 0.691

a jackknife procedure). Results for the first pair of canonical variates were impressively stable, with one exception. When transect number 16 was eliminated from the analysis, the loadings for the first pair of canonical variates were not interpretable (table 3). However, upon inspection I discovered that the second pair of canonical variates were loaded precisely in the same pattern as the first pair in all of the other rotations. Thus, the same patterns were present in all trials, but for some reason the second orthogonal pair of variates switched with the first when transect number 16 was deleted from the analysis. The second canonical correlation was statistically significant ($P < 0.05$) in this case whereas it was not in any of the other analyses.

The results of the robustness assessment are summarized in table 4 where the means and standard deviations of the canonical correlations and variable loadings are presented for 20 rotations. For the analysis where transect 16 was eliminated, the second pair of canonical variates was used, but for all other cases the results were averaged over the first pair of canonical variates.

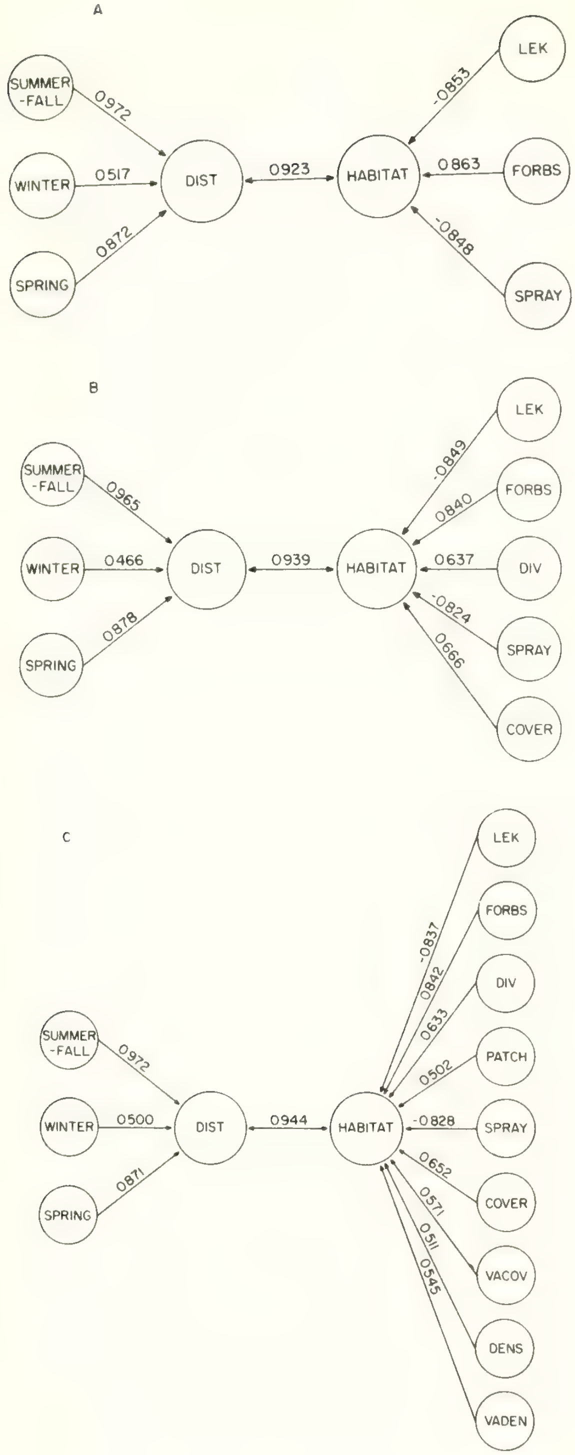

Figure 3. Path diagram of the first pair of canonical variates with three distribution variables and three (A), five (B), and nine (C) habitat variables. The significance levels based upon Bartlett's test are P = 0.00003, 0.00006 and 0.004 for the 3 x 3, 3 x 5, and 3 x 9 analyses respectively. Definitions of variables are listed in table 1.

To further assess the robustness of the 3 x 9 canonical correlation analysis, I systematically eliminated one of nine habitat variables from the analysis. The canonical correlations and variable loadings proved very stable for the first pair of canonical variates. In this experiment as well as during the rotation of cases, loadings into the second pair of canonical variates fluctuated dramatically. As can be seen in table 4, however, variation in canonical correlations and variable loadings for the first pair of canonical variates is impressively small.

The importance of distance to a lek is not clear from these results. It seems plausible that leks are located in good habitats but this may obscure results since grouse social behavior may override habitat quality in determining their distribution. My first attempt to better understand the importance of leks entailed using regression analysis to remove variation attributable to LEK from each of three distribution variables. Then canonical correlation analysis was conducted between the residuals of the distribution variables and the eight original habitat variables with LEK (sensu Boyce 1978). However, the canonical correlation was not statistically significant, and variable loadings were not interpretable. Further multiple regression analysis of the three distribution variables was conducted by studying residuals after removing variation attributable to the area in sprayed sagebrush habitat (SPRAY). The partial correlation between the fecal dropping variables and LEK was discovered to be significant only in the springtime ($r = -0.639$, $P < 0.01$). Since the leks are only actively used during March, April, and May, it seems plausible that only in spring should there be any unique contribution to distribution determined by the proximity to a lek.

DISCUSSION

Sample size guidelines are lacking for applications of many multivariate procedures. Although Bartlett's test for canonical correlation allows one to assess the overall significance of the relationship between two sets of variables, there is presently no means by which significance of individual variable loadings can be evaluated. Nevertheless, the most useful applications of procedures such as canonical correlation may be heuristic ones, thus inference procedures may not be necessary or even desirable. However, assessing the goodness of such descriptive tools does seem important, and robust procedures such as jackknifing provide such an assessment. If canonical correlations and variable loadings prove to be robust, as they were in this study, the extremely large sample sizes recommended by Thorndike (1978) should not be necessary. The impracticality of collecting extremely large data sets in wildife habitat studies should not persuade the investigator that applications of multivariate procedures, such as canonical correlation, are necessarily inappropriate.

Table 3. Correlation between original variables and the first two pairs of derived canonical variates when transect number 16 was eliminated from the analysis. Note the similarity between figure 3C and the loadings for the second pair of canonical variates. The probability levels are from Bartlett's test.

	Distribution variate		Habitat variate	
First Canonical	SUMMER-FALL	-0.542	LEK	0.090
r = 0.973	WINTER	-0.548	FORBS	-0.566
(P = 0.0002)	SPRING	-0.040	DIV	-0.229
			PATCH	-0.052
			SPRAY	0.544
			COVER	0.053
			VACOV	-0.041
			DENS	0.072
			VADEN	-0.082
Second Canonical	SUMMER-FALL	0.827	LEK	-0.858
r = 0.931	WINTER	0.424	FORBS	0.647
(P = 0.048)	SPRING	0.924	DIV	0.589
			PATCH	0.573
			SPRAY	-0.655
			COVER	0.707
			VACOV	0.567
			DENS	0.551
			VADEN	0.425

Cohen et al. (1979) claim that canonical weights (loadings) are necessarily unstable in canonical correlation because each variable accounts for a unique portion of the variability in the other set of variables. However, we have seen in this analysis that unstable loadings or "bouncing betas" need not occur and that removal or addition of variables need not influence the qualitative interpretation. It seems more likely that nonlinearity or multicollinearity are behind many applications where "bouncing betas" appear to be a serious problem (see Gauch and Wentworth 1976).

The results depicted in figure 3 confirm many of the subjective impressions which were developed based upon field obsevations of the major habitat components important to sage grouse. During winter, sage grouse feed exclusively on leaves of big sagebrush (Artemisia tridentata). However, between April and October, forbs such as dandelion (Taraxacum officianale), curly-cup gumweed (Grindelia squarrosa), sweet clover (Melilotus officianalis), false dandelion (Agoseris glauca), alfalfa (Medicago sativa), and salsify (Tragopogon dubius) constitute a major portion of the diet for both young and adult birds (Patterson 1952). Although sagebrush provides important visual cover from aerial predators, sagebrush plants compete with forbs for nutrients and water. Thus optimal habitats are often patchy where forbs and sagebrush cover occur in close proximity.

Each of the variables which we selected to measure habitat patchiness (DIV, PATCH, VACOV, VADEN) is positively correlated with the number of droppings found on the transects. Similarly, these same variables are positively correlated with the "habitat quality" variate. SPRAY is clearly an important variable which is negatively loaded into the "habitat quality" variate. Since spraying with herbicides such as 2,4-D kills both forbs and sagebrush, it is easy to appreciate the devastating impact of herbicide spraying on the use of areas by sage grouse.

It is important to caution against cavelier interpretations of canonical correlation analysis. As noted earlier, explicit hypothesis testing regarding any single variable is not possible with canonical correlation but may be accomplished with linear regression techniques. Some patterns can be masked by simple reliance upon the overall trends summarized by canonical correlation as I demonstrated above for LEK. Also, to achieve a robust canonical model, variables must often be eliminated for statistical reasons even though some of these variables may be biologically important, e.g., SAGE. I strongly recommend that careful attention be given to any variables of postulated biological significance but which must be eliminated on statistical grounds. Various statistical procedures may provide insight into the behavior of these variables, e.g., nonlinear regression, ridge regression, discriminant analysis, or nonparametric techniques.

In summary, my application of canonical correlation does not provide much insight into the

Table 4. Robust estimates of canonical correlations and variable loadings. The top portion of the table lists means and standard deviations (in parentheses) of values where one case (transect) was systematically eliminated from the analysis (n = 20). The bottom portion lists means and standard deviations when one habitat variable was eliminated (n = 9).

	Distribution variate		Habitat variate	
Rotation of Cases				
Canonical	SUMMER-FALL	0.957(0.036)	LEK	-0.827(0.051)
$\bar{r}$ = 0.950(0.011)	WINTER	0.488(0.063)	FORBS	0.826(0.047)
($\bar{P}$ = 0.0077[0.005])	SPRING	0.864(0.062)	DIV	0.625(0.043)
			PATCH	0.498(0.059)
			SPRAY	-0.811(0.048)
			COVER	0.646(0.068)
			VACOV	0.564(0.065)
			DENS	0.539(0.08)
			VADEN	0.502(0.075)
Rotation of Habitat Variables				
Canonical	SUMMER-FALL	0.969(0.024)	LEK	-0.837(0.019)
$\bar{r}$ = 0.940(0.003)	WINTER	0.506(0.065)	FORBS	0.839(0.014)
($\bar{P}$ = 0.007[0.014])	SPRING	0.846(0.069)	DIV	0.630(0.012)
			PATCH	0.497(0.012)
			SPRAY	-0.838(0.015)
			COVER	0.634(0.061)
			VACOV	0.558(0.046)
			DENS	0.527(0.073)
			VADEN	0.495(0.060)

interactions between sage grouse distribution and habitat that I could not glean from multiple regression analysis. This is not surprising since canonical correlation is somewhat of a generalization of multiple regression (Blackith and Reyment 1971). However, canonical correlation does provide a succinct and synoptic way to summarize a bulky and unwieldly data set. This is certainly one of the most important functions of multivariate statistical analysis.

ACKNOWLEDGMENTS

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ECOLOGICAL RELATIONSHIPS OF GRASSLAND BIRDS TO HABITAT AND FOOD SUPPLY IN EAST AFRICA[1]

L. Joseph Folse. Jr.[2]

Abstract.--Canonical correlation analysis was used to evaluate relationships between 17 species of grassland birds, structural parameters of the grassland habitat, and biomasses of 25 age-taxonomic categories of arthropods in a study of ecological relationships of grassland birds in the Serengeti National Park, Tanzania, East Africa. The bird-habitat analysis resulted in correlations that were interpretable both in terms of identifiable characteristics of the habitat and in terms of identifying specific groups of birds which exploited the habitat in similar ways. The bird-arthropod analysis produced correlations which were not easily interpretable relative to arthropod characteristics nor in terms of identifying groups of birds based on their association with the arthropod resource. A canonical correlation of birds with habitat plus arthropod variables had results similar to that of the bird-habitat analysis and dissimilar to the bird-arthropod analysis. These results suggest that mechanisms affecting the guild structure of grassland birds in the Serengeti are more likely associated with habitat structure than with food supply.

Key words: Arthropods; canonical correlations; grassland birds; habitat selection; multivariate analysis; Serengeti; Tanzania.

INTRODUCTION

The use of multivariate statistics in evaluating ecological relationships of birds has expanded considerably in recent years. One problem of importance that is often approached with multivariate methods is that of evaluating the structure of bird communities relative to their exploitation of habitat and/or food resources. The multivariate technique which is most suited to exploring relationships between two such groups of variables, e.g., community composition and niche parameters, is that of canonical correlation (Gittens 1979, Kshirsagar 1978, Morrison 1976). However, this technique seems to have been used little in ornithology, perhaps due to lack of adequate data from field studies.

This study illustrates an attempt to use canonical correlation analysis to identify and evaluate some relationships between grassland birds and their habitat and food supply on the Serengeti plains, Tanzania. At the outset of the study, little was known about the community composition or densities of the birds, nor about their habitat relations. Consequently, this analysis was designed to treat the following objectives: 1) to determine if there is a structural organization of the avifauna that is related to characteristics of the habitat and arthropod fauna, 2) to define recognizable groups of bird species whose members are similarly associated with habitat and arthropod characteristics, and 3) to identify specific characteristics of the habitat and arthropod fauna which may potentially affect this avifaunal structure. Objective 1 can be met by determining if there are significant canonical correlations between the birds and the environmental parameters. If groups of bird species are recognizable based on their correlations with significant canonical variates, then these may be considered as guilds due to the similarity of these species in exploiting resources, and this would satisfy Objective 2. Objective 3 may be met if the canonical variates are interpretable in terms of their associations with the habitat and arthropod variables of the analysis.

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STUDY AREAS

The field study took place from May 1975 to April 1976 in the Serengeti National Park, Tanzania. Five 1-km² study sites were established to represent a range of grassland vegetation conditions in the plains portion of the park (fig. 1). Detailed descriptions of each site are available in Folse (1978). Precipitation in the Serengeti was seasonal and highly variable, both in time and space; there was an increasing gradient in precipitation from the southeast to the northwest (with 500 mm to 700 mm per anum on the plains). This variation in precipitation, coupled with intensive seasonal grazing by wildebeests, zebra, gazelle, and others, and dry season fires, resulted in a great degree of variation in vegetation structure among the different sites. Within each of the sites, however, the structure of the vegetation was reasonably uniform with major variation taking place through time (seasonally).

METHODS

The data used in these analyses were based on concurrent samples of numbers of birds of each species in the community, structural parameters of the vegetation, and numbers of arthropods in several age-taxonomic classes. Details of the sampling procedures are described in Folse (1978). These samples were taken at monthly intervals at each of the study sites (two samples were missing resulting in 58 observations). Bird numbers were sampled at each site with nine systematic transects (in groups of three). Each transect was 1 km long and 20 m wide; they were run in a vehicle and the number and identity of each bird species flushed from the transect was recorded. The sampling intensity was 18% of each study area. The bird data were converted to biomass estimates based on sampled weights and were then log-transformed prior to analysis; preliminary analyses indicated that mean values and variances of untransformed biomasses (of all biomass variables in the study) were proportional, suggesting the need for such a variance stabilizing transformation prior to analysis.

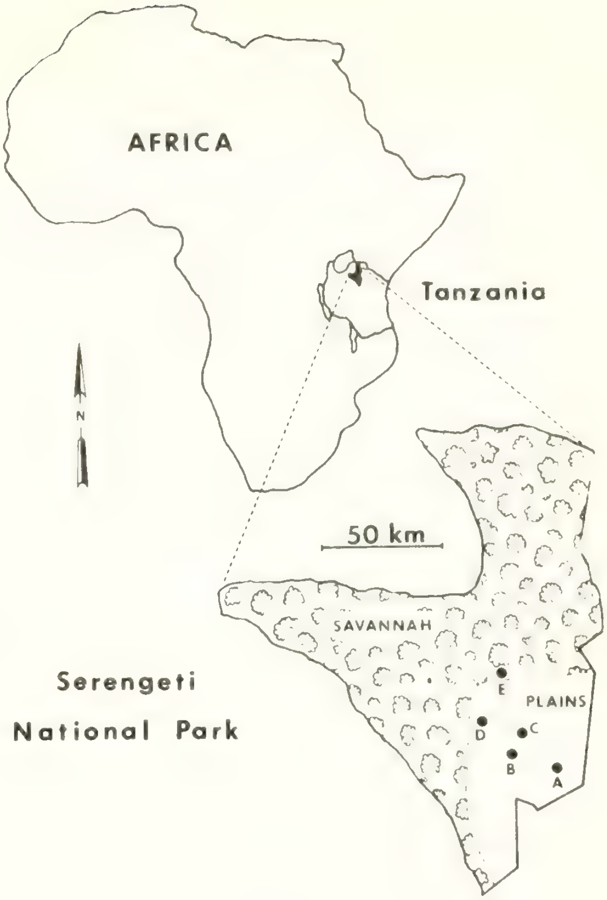

Figure 1. Location of the study sites (A through E) in the plains portion of the Serengeti National Park, Tanzania.

Arthropod data were collected on four sweep-net transects placed systematically on each study site. Fifty sweeps were made on each transect. Size distributions of 25 age-taxonomic categories of arthropods were available for each transect, and these were converted to biomass estimates based on sampled length-weight relationships for each group. Arthropod biomass data were also log-transformed prior to analysis.

Habitat data were collected from four transects associated with the arthropod samples. Six sample units at 20-pace intervals were used for each transect. At each sample unit, four sample points were placed in a square with 2 m diagonals. At each sample point, a thin wire was placed vertically, and the number of contacts of vegetation (both total and green) with the wire was recorded in 10 cm intervals above the ground. In addition, maximum height of emergent vegetation within a 1 m radius of the center of the sample unit was recorded. From these samples, I calculated indices of total biomass, green biomass, percent cover, percent vegetation below 10 cm (an index of vertical vegetation structure), and vegetation height. Two additional variables were created by using values of total and green biomass lagged by one month; these variables were included to evaluate possible delayed response of birds to changes in the vegetation biomass variables. Accumulated precipitation (monthly intervals) data were available from storage gauges near each site. All biomass data were log-transformed and all the percentage data were transformed with the arcsin square root transformation (Sokal and Rohlf 1969).

Canonical correlations were run on appropriate subsamples of the data set (with monthly mean values) with the CANCORR procedure of SAS (Barr et al. 1979). I shall refer to a linear compound of original variables produced by the procedure CANCORR as a canonical variate, and coefficients of the variates associated with each original variable as factors. In two-group canonical analysis, pairs of canonical variates are produced. Each variate pair contains one variate of bird factors and one variate of environmental (habitat and/or arthropod) factors. The first pair has a maximum possible correlation. The second pair is maximally correlated, given that each is orthogonal to its corresponding variate in the first pair, and so on. Usually, only the "significant" correlations and their corresponding variate pairs are considered in evaluation of the relationships. In the usual approach to canonical analysis, the observations are plotted in variate space using either set of variates, and these observations are then clustered to look for relationships among the observations in the variate space. Thus variates are used to establish relationships among observations, and canonical correlations are used as a measure of how well the two sets of variates provide the same set of relationships among observations (site-time combinations in the present case). Interpretation of what each variate "means" is usually accomplished by considering simple correlations of each of the variables with the variate.

In the present study, emphasis was on the bird community rather than on the observations (site-time combinations); thus I wished to use canonical correlation as a technique of classification or ordination based directly on relationships of the bird species to environmental variables rather than indirectly through "association" or "distance" relationships among the birds themselves. Consequently, rather than group observations based on variate factors (as is usually done), I sought to group species of birds based on their simple correlations with the variates, using the variates as a means of establishing structural relationships between birds and environmental variables (fig. 2).

In addition to the analyses described above, I tested the homoscedasticity of the variance-covariance matrices with Wilk's generalized likelihood ratio test described by Morrison (1976:250, eq. 4). A canonical correlation also was run with all data with the variables standardized.

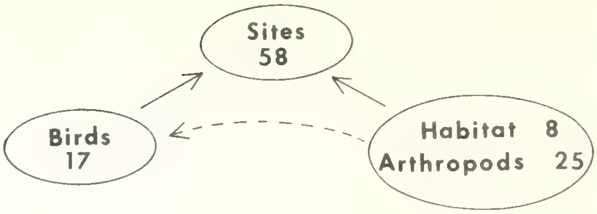

Figure 2. Relationships among bird species, environmental variables, and site-time (sites) structure of the data set. Environmental variables potentially affect composition of the bird fauna via conditions at the sites. Numbers indicate number of variables for birds and environmental characteristics and number of observations for sites.

RESULTS

Seventeen species of grassland birds were considered as study species (table 1). These were fairly small birds which depended on the grassland habitat for most of their requirements and were not dependent on specialized microhabitats such as trees, waterholes, etc. The energy requirements of these birds were satisfied mainly by arthropods (estimated 81%, Folse 1978), thus I considered arthropods as the primary food resource of the birds used in this analysis (although one species is almost wholly granivorous).

The first canonical analysis involved 17 species of birds versus all environmental variables (8 habitat and 25 arthropod). Six "significant" canonical correlations resulted with bird variates that explained 57% of the variance in the bird portion of the data set; 45% of that variance was explained by the first three correlations (table 2). Simple correlations of each bird variable with bird variates were used to determine the coordinates of each species in the correlation space associatied with the first three bird variates (fig. 3). This produced six recognizable groups of birds, each consisting of species which were associated with the environmental variables in similar ways (fig. 3).

Interpretation of the environmental variates produced by the first canonical analysis may be accomplished by examining correlations of environmental variables with environmental variates (table 3). The first variate had negative associations with high vegetation biomass, high vegetation cover, tall vegetation, and with vertical vegetation structure (the latter indicated by the positive association with percent vegetation below 10 cm). It also had negative correlations with shorthorned grasshopppers(ACRA, ACRN), spiders (ARAU), crickets (GRYU), bugs (HEMA), and caterpillars (LEPN). This variate may be interpreted as a gradient between short grass, low vegetation biomass versus tall grass, high vegetation biomass with corresponding low versus

Table 1. Common names (scientific name) of bird species considered in this study.

1.	Crowned lapwing	*Vanellus coronatus*
2.	Caspian plover	*Charadrius asiaticus*
3.	Two-banded courser	*Cusorius africanus*
4.	Northern white-tailed bush-lark	*Mirafra albicauda*
5.	Rufous-naped lark	*Mirafra africana*
6.	Flappet lark	*Mirafra rufocinnamomea*
7.	Fawn-colored lark	*Mirafra africanoides*
8.	Red-capped lark	*Calandrella cinerea*
9.	Fisher's sparrow-lark	*Eremopterix leucopareia*
10.	Short-tailed lark	*Pseudalaemon fremantlii*
11.	Richard's pipit	*Anthus novaeseelandiae*
12.	Sandy plain-backed pipit	*Anthus vaalensis*
13.	Yellow-throated longclaw	*Macronyx croceus*
14.	Rosy-breasted longclaw	*Macronyx ameliae*
15.	Capped wheatear	*Oenanthe pileata*
16.	Rattling cisticola	*Cisticola chiniana*
17.	Wing-snapping cisticola Zitting Cisticola	*Cisticola ayresii* *Cisticola juncidis*[1]

[1] These two species had broadly overlapping ranges and were indistinguishable in flight during the sample censuses.

high biomass gradient of these arthropods. The second variate was associated with low cover, low vegetation biomass (lagged) versus high cover, high vegetation biomass which was independent of vegetation height. It had no strong associations with arthropods. The third variate had a weak positive association with grasshoppers (ACRA, ACRN, TTRU) but no strong association with any of the other environmental variables. Precipitation was unimportant relative to these variates and green vegetation biomass was weakly associated with the first variate.

The second canonical analysis involved birds versus eight habitat variables. This resulted in three "significant" correlations in which the bird variates explained 39% of the variance in the bird portion of the data set (table 2). A plot of bird correlations with bird variates resulted in a group structure similar to that of the first analysis with all environmental variables (fig. 4). Bird species 12, the sandy plain-backed pipit, was less strongly associated with the "woodland" group and the "short-grass-plains" group (species 2, the Caspian plover, and species 15, the capped wheatear) was less distinctly defined. Interpretation of environmental variates was similar to that of the complete analysis (without arthropods).

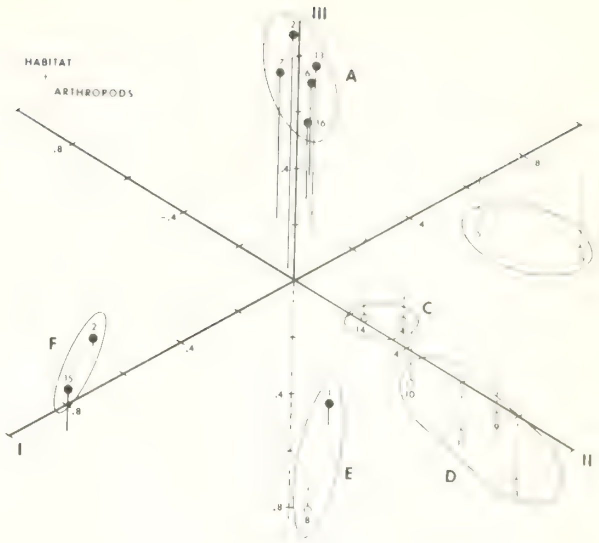

Figure 3. Bird species group structure resulting from simple correlations of bird species with the first three bird canonical variates from the complete canonical analysis (with all environmental variables included). Points below the horizontal plane of the three-dimensional plot have dashed lines and open circles. Groups indicated are potential guilds whose members are associated with environmental characteristics in similar ways. Numbers correspond to those in table 1. Group A is the "woodland" group; B the "tall-grass" group; C the "clumped-grass" group; D the "low-cover" group; E the "plains" group; and F the "short-grass-plains" group.

The third canonical analysis involved birds versus arthropod variables (habitat variables excluded). This resulted in four "significant" correlations in which bird variates explained 37% of variance in the bird portion of the data set (31% for the first three variates, table 2). A plot of bird correlations with bird variates (fig. 5) resulted in a completely different organization of bird species with a much less definite group structure. I can recognize 6 groups (fig. 5), only one of which occurred in the complete analysis (the "tall-grass" group—species 5, the rufous-naped lark, and species 17, the wing-snapping/zitting cistiocolas).

Canonical correlation of the full model with standardized variables resulted in different canonical variates, but identical canonical

Table 2. Canonical correlations and percent variance[1] of bird biomasses accounted for by each bird canonical variate.

	Birds vs. Habitat + Arthropods		Birds vs. Habitat		Birds vs. Arthropods	
Canonical variate	Canonical correlation	Variance %	Canonical correlation	Variance %	Canonical correlation	Variance %
1	0.999	19.1	0.984	19.6	0.987	17.9
2	0.995	14.1	0.904	13.4	0.969	5.9
3	0.989	11.9	0.802	6.4	0.954	7.3
4	0.972	3.2			0.939	5.6
5	0.963	4.6				
6	0.950	4.5				
		57.4%		39.4%		36.7%

[1] Percent variance = $(1/k)(\sum_j r_{ij}^2)$, where r_{ij} is the correlation of the j^{th} species with the i^{th} bird canonical variate and k is the number of bird species (17 in this case).

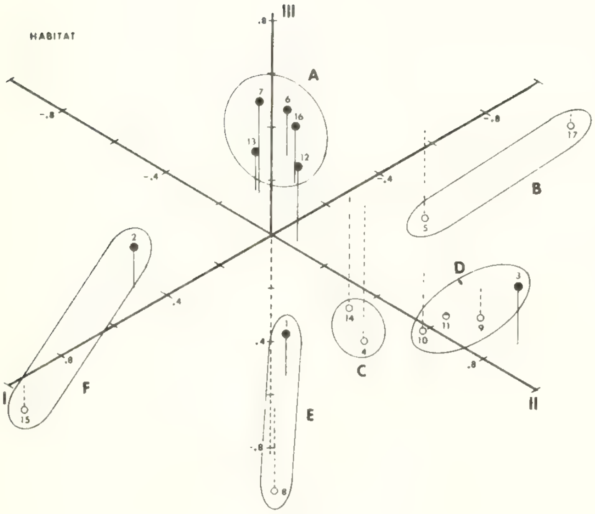

Figure 4. Simple correlations of birds species with the first three bird canonical variates with habitat variates only. See figure 3 for a detailed description. Note that group structure is similar to that of figure 3.

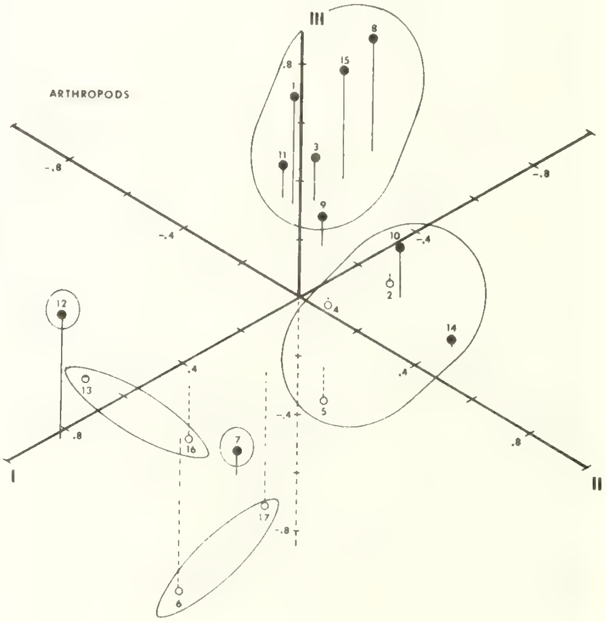

Figure 5. Simple correlations of bird species with the first three bird canonical variates with anthropod variables only. See figure 3 for a detailed description. Note that group structure is much different from that of figures 3 and 4.

Table 3. Simple correlations of environmental variables with the first three environmental canonical variates.

	Canonical variate		
	I	II	III
Habitat:			
Total vegetation	-0.72	-0.43	-0.09
Green vegetation	-0.41	0.17	0.09
Percent cover	-0.51	-0.58	0.00
Percent veg.< 10cm	0.89	-0.04	0.20
Height	-0.89	-0.21	-0.23
Precipitation	-0.15	0.07	0.23
Tot. veg. (lagged)	-0.69	-0.50	-0.18
Gr. veg. (lagged)	-0.41	0.10	-0.12
Anthropods[1]:			
ACRA	-0.53	-0.38	0.41
ACRN	-0.52	-0.32	0.46
ARAU	-0.63	-0.31	-0.08
BLAA	-0.22	0.19	-0.16
BLAN	-0.29	0.15	-0.03
COLA	-0.37	-0.15	0.19
DIPA	-0.47	-0.17	0.13
FORA	-0.17	0.16	-0.15
GRYU	-0.67	-0.20	-0.11
HEMA	-0.52	-0.17	0.08
HEMN	-0.32	-0.25	-0.06
HOMA	-0.56	0.21	-0.03
HOMN	-0.34	-0.09	-0.11
HYMA	-0.28	0.03	0.03
ISOA	-0.14	0.17	-0.17
LEPA	-0.11	0.02	0.07
LEPN	-0.55	-0.23	0.09
MANA	-0.08	0.22	-0.10
MANN	-0.47	-0.22	0.03
NEUA	-0.08	-0.32	-0.19
OTHU	-0.05	0.08	-0.08
PHSU	-0.36	-0.02	-0.21
TETA	-0.27	-0.14	-0.02
TETN	-0.34	-0.12	0.03
TTRU	-0.33	0.04	0.63

[1] First three letters of each name symbol correspond to arthropod order or family name; last letter refers to age category: A = alate (winged adult), N = nonalate, and U = unknown (both A and N). Thus ACRA stands for Acrididae alate. OTHU is "other".

correlations and identical simple correlations of the standardized variables (as the original variables) with their corresponding variates (as expected). Results of tests of homoscedasticity of variance-covariance matrices showed that all matrices were not homoscedastic.

DISCUSSION

The question of whether or not there is a structural organization to the avifauna related to characteristics of habitat and arthropod fauna (Objective 1) can be answered affirmatively; results of all the canonical correlation analyses demonstrated it. The bird with habitat and the bird with habitat-arthropod analyses produced the same recognizable groups of bird species (Objective 2). The bird with arthropod analysis, however, produced a different organization of bird species with no clear group structure. In the complete analysis, the group structure was due primarily to the habitat characteristics rather than the arthropod characteristics, since removing arthropods from the analysis produced very little change while removing habitat characteristics led to great change in the resulting structure.

The complete analysis led to six groups of birds. The "woodland" group consisted of six species which occurred primarily at site E on the woodland-plains border. The "low-cover" group had four species which occurred throughout the Serengeti plains but were usualy in areas with extensive open ground and little ground-level obstruction. Tall grass could occur in these areas, but it was usually sparsely distributed. The "tall-grass" group (two species) occurred throughout the plains but always in association with tall grass (they were rare at site A). The greater the vertical vegetation structure and vegetation density, the greater the density of these species. The "clumped-grass" group (two species) occurred mostly at sites C and D, and were always associated with fairly dense clumps of vegetation. The "short-grass-plains" group (two species) occurred mainly at site A with little or no vertical vegetation structure, but with reasonably high percent cover. The "plains" group (two species) had a broad range throughout the Serengeti plains, but were usually associated with areas of short vegetation, low cover, and fairly reduced vegetation biomass. Three of these groups (woodland, clumped-grass, and short-grass-plains) were fairly restricted in the range of sites they used while the remaining groups (low-cover, tall-grass, and plains) each had quite broad ranges with respect to sites. However, each used specific types of microhabitat within sites and/or used a site at times of the year when habitat conditions were suitable. Each of these six groups is a good candidate for a guild (a group of species which exploit their environmental resources in similar ways). Objective 2 seems to be well satisfied.

Objective 3 has been partially satisfied by the fact that habitat variables and not arthropod variables are most important in the organization of the avifaunal group structure. Consideration of simple correlations of habitat and arthropod variables with the corresponding canonical variates suggested that the variables of most importance were vegetaion biomass, percent cover, height, and vertical structure of the vegetation. Green vegetation biomass and lagged values of vegetation biomass were also of importance. The importance of the lagged values suggests that there is some degree of inertia in the response of the birds to changes in habitat conditions.

Precipitation, per se, was unimportant. The most important arthropod variables, although minor, were grasshoppers, spiders, crickets, bugs and caterpillars.

The canonical correlation analyses of these data seemed to be very satisfactory relative to the original objectives, but were they appropriate? I had a total of 50 variables (worst case) and only 58 observations. While the number of observations was sufficient to allow the analysis to be completed technically, it was "data-poor." Thus, as an estimation technique for population parameters, the analysis would be weak but to establish relationships within my data set, the sample size was adequate, provided that "significance" of the resulting canonical correlations is regarded with caution. Since this was an exploratory analysis to look for potential relationships among bird species for further analysis and study, the technique seemed useful.

Williams (1981) pointed out that heteroscedasticity of the variance-covariance matrix used in canonical correlation analysis can lead to biased estimates of factors (coefficients of the canonical variates) and to different relationships of observations when they are plotted in canonical space versus observation space. However, these problems are much less important when considering group structure of one variable set based on simple correlations with resulting variates. This is evident from the fact that both unstandardized and standardized variables resulted in the same correlation structure whereas the corresponding canonical variates were different. However, standardizing normalized variables individually does not necessarily produce homoscedasticity since no consideration is taken of the covariance structure of the data. Although the variance-covariance matrices used in these analyses were heteroscedastic, the fact that most variables were transformed with traditionally normalizing transformations, and the correlations rather than variate factors were used in establishing avian groups, should have led to a fairly stable analysis. Dropping out half of the variables for the habitat analysis (the arthropod variables) resulted in little change in the avifaunal group structure, which suggests that heteroscedasticity characteristics of the arthropod portion of the variance-covariance matrix had little effect in biasing the results.

ACKNOWLEDGMENTS

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DISCUSSION

NOVA SILVY: Could arthropods be correlated with the vegetation structure in a manner such that they contributed nothing new to the analysis when they were added into the data sets?

L. JOSEPH FOLSE, JR.: The arthropod distribution is very much determined by the vegetation distribution; however, the relationships do not seem to be concordant with the bird-habitat relationships. If they were, the bird-arthropod canonical correlation would not result in a completely different organizational structure.

HABITAT ASSOCIATIONS OF BIRDS BREEDING IN CLEARCUT DECIDUOUS FORESTS IN WEST VIRGINIA[1]

Brian A. Maurer[2], Laurence B. McArthur[3], and Robert C. Whitmore[4]

Abstract.--Associations between vegetation structure and 34 bird species in four forested areas of various stages of clearcut regrowth were examined using principal components analysis. Relative frequencies for each bird species were determined during three breeding seasons and used to weight habitat variables. The resulting data matrix (34 species x 8 habitat variables) was subjected to principal components analysis using a standardized covariance matrix.

The first principal component was negatively correlated with percent and mean height of low vegetation, and positively correlated with percent litter and the number, height, and percent of canopy layers. The first principal component separated early successional species from late successional species. The second principal component was positively correlated with percent slash and the number of trees less than 12.7 cm dbh. This component separated mid-successional species from earlier and later successional species. The first two components explained 90% of the variation and thus seemed to be an adequate description of the habitat associations of most species. The third component, however, was useful in separating a few of the mid-successional species, with species that foraged mainly on the ground having higher values than species that foraged on small trees and shrubs. The third component was positively correlated with percent litter and negatively correlated with the number of trees less than 12.7 cm dbh. Field methods used in this study appear to be most applicable where it is impractical to use more conventional methods of collecting habitat association data, e.g., territory mapping, or use of male singing perches.

Key words: Clearcut; deciduous forests; habitat associations; habitat ordination; nongame management; passerine birds; principal components analysis; West Virginia.

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INTRODUCTION

Current field techniques for assessing habitat relationships are based on measuring habitat variables in activity centers of individual organisms. In the case of birds, male singing perches are often used to determine activity centers. This paper presents another method of obtaining habitat association data that can be used to compare overall habitat preferences of bird species breeding in several different habitats. The procedure analyzes variation between species by obtaining a mean value for each species for each of several habitat variables, and subjecting the resulting data matrix to a principal components analysis.

STUDY AREAS

Data on bird populations and habitat structure were collected on four watersheds in the Fernow Experimental Forest, 4.8 km southeast of Parsons, Tucker Co., West Virginia. The watersheds have been used by the USDA Forest Service to assess impacts of various logging and herbicide treatments on forest hydrology. Logging and herbicide treatments have created several different habitats which attract different bird communities.

Watershed 4 (WS4), a 39-ha area used as a control in the hydrology experiments, was logged in 1911, and has remained relatively untouched since then. Trees killed by chestnut blight were salvaged during the early 1940's. Tree species common in this area included sugar maple, red maple, red oak, chestnut oak, black birch, black cherry, American beech, and yellow poplar (scientific names of plants and birds are given in appendix I).

Watershed 3 (WS3), 34 ha in size, was clearcut between July 1969 and May 1970, except for a strip of trees along the main drainage. Remaining trees were removed during the winter of 1972-1973, and the area has revegetated naturally since then. Tree species common in this area included saplings of many mature forest species, as well as sassafras and pin cherry.

Watershed 7 (WS7), a 24-ha watershed, was partially clearcut in 1964, and regrowth was suppressed with herbicide treatments until 1967, when the rest of the watershed was clearcut. The area was kept barren for another 2 years before allowing regrowth to resume. Saplings of several mature forest trees were common in this area. Sassafras and pin cherry were also present, however, staghorn sumac was common in the watershed.

Watershed 6 (WS6), 22 ha, was treated with herbicides in a manner similar to WS 7. The watershed has been further treated with herbicides several times since 1971 to discourage natural hardwood and herbaceous revegetation, and to encourage establishment of Norway spruce. This area had a dominant ground cover of ferns, with several species of saplings and blackberry occurring sporadically throughout the watershed.

Table 1. Three-year means for vegetation structure variables in each watershed.

Variable	WS4	WS3	WS7	WS6
Litter (%)	87.3	83.6	68.7	59.7
Slash (%)	7.6	17.2	11.7	11.3
Herbaceous vegetation (%)	42.2	24.7	78.9	85.7
$\bar{X}$ height herb. veg. (cm)	27.9	29.7	61.7	59.3
Canopy layers (no.)	2.1	1.4	1.1	0.2
Max. canopy height (m)	21.3	6.7	4.3	2.1
Canopy cover (%)	96.8	90.9	77.8	4.9
Trees <12.7 cm (no.)	0.6	2.3	1.1	0.2

METHODS

Avian populations were censused during the breeding seasons of 1977, 1978, and 1979 using 30-m belt transects established in each area. All areas were visited about the same number of times each year. Transects were walked between sunrise and 0730 EDT at a predetermined pace, and the number of singing males of each bird species was recorded.

On 1m x 1m plots located randomly within the belt transects, 13 vegetation characteristics were measured in each watershed during July. In statistical analyses, only eight variables (table 1) were actually used to minimize duplication of information.

We assumed that vegetation characteristics prevalent in a watershed during a given year directly or indirectly influenced the relative abundance of bird species in that watershed. Making this assumption, we weighted the mean value of each habitat variable by relative frequency of a bird species in a watershed for each year. Years in which a species was more common in a watershed were weighted more than years in which a species was relatively less common. This was accomplished by dividing relative frequency of a species for a given watershed-year combination by the sum of all relative frequencies for that species over the 12 watershed-year combinations. This procedure is illustrated for the red-eyed vireo in table 2.

Table 2. Relative frequency of red-eyed vireos (RF_i) and mean % canopy cover ($\bar{X}_i$) for 3 years in four watersheds. The procedure of obtaining weighted mean values ($\bar{X}_w$) used in principal components analysis is illustrated by these data.

Year	Watershed	RF_i	$\bar{X}_i$
1977	4	0.32	92.7
	3	0.06	84.6
	7	0.02	66.0
	6	0	6.0
1978	4	0.49	98.7
	3	0.23	94.2
	7	0.15	84.2
	6	0.02	2.5
1979	4	0.23	99.4
	3	0.28	95.6
	7	0.19	88.0
	6	0.04	5.0

$$\Sigma \; RF_i = 2.03$$

$$\bar{X}_w = \frac{\sum_{i=1}^{12} RF_i \bar{X}_i}{2.03} = 91.3\%$$

Entries in the data matrix (34 species x 8 habitat variables) to be used for a principal components analysis were weighted mean values for each habitat variable for each species. Calculations described above were done using the PROC MATRIX procedure of Statistical Analysis System (SAS, Helwig and Council 1979). A correlation matrix for the habitat variables was calculated and a principal components analysis (PCA) was done on PROC MATRIX using a program written by the second author. Output included eight eigenvalues and eigenvectors, correlations of original variables with each principal component, scores for each bird species on the principal components, and a plot of species scores on the components. Copies of the PCA program are available from the authors.

RESULTS

Means for all habitat variables are given in table 1. Inspection of these data were useful in obtaining an overall impression of the structural characteristics of each watershed.

Results of the PCA (table 3) indicated that the first three principal components accounted for most variation between bird species in their associations with habitat variables. Correlations of original variables with the first three components demonstrated that variables which tended to have high values in WS4 (mature forested watershed) were positively correlated with the first component, and variables with low values for WS4 were negatively correlated with the first component (table 3). The second principal component was significantly correlated with variables that either had high values or low values for WS3, a mid-successional area.

Table 3. Results of principal components analysis using weighted averages of 8 habitat variables for 34 bird species.

Component	1	2	3
Variation explained	67.46%	23.47%	5.50%
Cumulative variation	67.46%	90.93%	96.43%
Variable	**Correlations with original variables**		
Litter	0.85**	0.23	0.42**
Slash	-0.38*	0.86**	0.32
Herb. veg.	-0.93**	-0.29	0.07
$\bar{X}$ ht. herb. veg.	-0.96**	-0.01	-0.04
Canopy layers	0.98**	-0.14	0.01
Max. canopy ht.	0.90**	-0.41*	0.08
Canopy cover	0.95**	0.11	-0.20
Trees < 12.7 cm	0.27	0.90**	-0.33*

* $P < 0.05$, ** $P < 0.01$

A plot of species scores on the first two principal axes indicated that species were separated into three distinct groups (fig. 1). The first group had low scores on the first two components and was representative of species which preferred early-successional or open habitats. Some of these species, such as song sparrows and prairie warblers, were exclusively limited to WS6 and WS7 (McArthur 1980). The second group had high scores for the first principal component, and low scores on the second principal component. The group was composed of species which were primarily mature forest species. The third group had high values for both components and included species typical of mid-successional habitats.

The third principal component explained about 6% of the variation. This component separated some of the early to mid-successional birds from each other. Species which forage primarily from trees and shrubs, such as Canada warblers (Bent

1953) had negative scores on this axis, while ground foraging birds, such as brown thrashers and rufous-sided towhees (Bent 1968), had positive scores. The third principal component was postively correlated with litter and negatively correlated with number of small trees.

DISCUSSION

Previous methods of collecting habitat association data for birds have been to locate an activity center of an individual and measure habitat variables at that spot. In several studies, habitat variables have been measured on small plots (0.05 ha) centered around perches where singing males were observed (James 1971; Whitmore 1975, 1977; Smith 1977). However, the physical structure of some habitats restricts the ability of observers to approach perches of singing males, and could introduce a bias during data collection. For example, in eastern deciduous forests, early stages of regrowth produce dense stands of saplings laced with greenbriar and other deterrents to movement. WS3 in the present study was such an area. Though we could easily hear singing males, the problems in setting up even a small plot were formidable. Another method of obtaining habitat association data has been to locate territories (McArthur 1980, Rice 1978) or nests (Wray and Whitmore 1979) and measure vegetation in these areas. Again, in some habitats the physical structure of vegetation may impede efforts to collect data. The method we have presented alleviates many logistical difficulties that might be encounterd while collecting habitat association data in areas such as WS3.

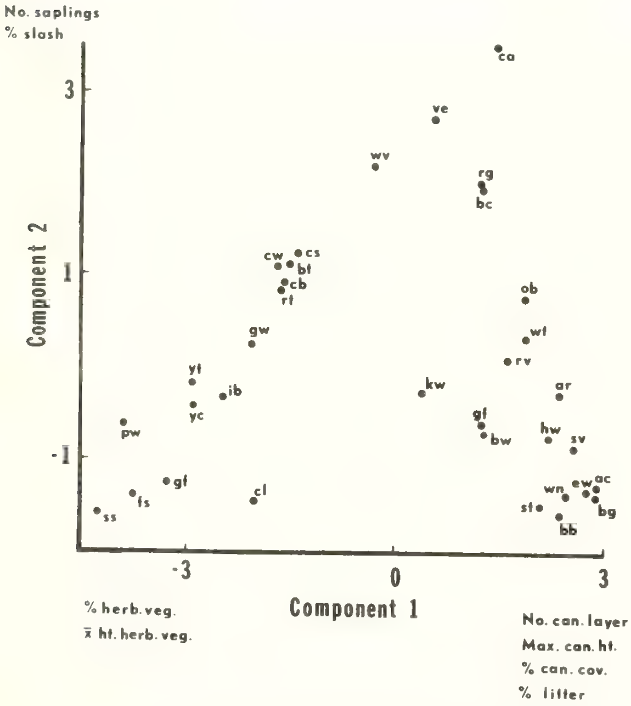

Figure 1. Ordination of 34 bird species on the first two principal components obtained from a PCA of 8 habitat variables. Species codes given in appendix.

Limitations of our analysis are as follows. First, the resolution obtained may not be as fine as might be desired in some situations. From a theoretical viewpoint, small differences in habitat preference between ecologically similar species may not be distinguishable. Also, though the method is suggestive, it is not strictly predictive. In addition, the problem of measuring the appropriate variables is always present. This problem can be partially alleviated by using literature to obtain ideas as to which habitat variables might be important. Finally, this method does not analyze within-species variation.

This method of assessing habitat associations should be useful in habitat management. Specific information is summarized by such an analysis on types of habitat characteristics a given bird species is associated with. Though this does not necessarily imply a cause-effect relationship between habitat variables and bird species abundanace, information provided by the PCA can give at least a rough estimate of how species will respond to alterations of habitat due to land use practices.

ACKNOWLEDGMENTS

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Appendix I

Scientific names of bird and plant species mentioned in the text. Codes for birds given in parentheses.

Birds

Great-crested flycatcher (gf)	*Myiarchus crinitus*
Acadian flycatcher (ac)	*Empidonax virescens*
Eastern wood pewee (ew)	*Contopus virens*
Black-capped chickadee (bc)	*Parus atricapillus*
White-breasted nuthatch (wn)	*Sitta carolinensis*
Gray catbird (cb)	*Dumetella carolinensis*
Brown thrasher (bt)	*Toxostoma rufrum*
Wood thrush (wt)	*Hylocichla mustelina*
Veery (ve)	*Catharus fuscescens*
Cedar waxwing (cw)	*Bombycilla cedrorum*
Solitary vireo (sv)	*Vireo solitarius*
White-eyed vireo (wv)	*V. griseus*
Red-eyed vireo (rv)	*V. olivaceus*
Black-and-white warbler (bw)	*Mniotilta varia*
Golden-winged warbler (gw)	*Vermivora chrysoptera*
Black-throated green warbler (bg)	*Dendroica virens*
Black-throated blue warbler (bb)	*D. caerulescens*
Chestnut-sided warbler (cs)	*D. pensylvanica*
Prairie warbler (pw)	*D. discolor*
Ovenbird (ob)	*Seiurus aurocapillus*
Common yellowthroat (yt)	*Geothlypis trichas*
Yellow-breasted chat (yc)	*Icteria virens*
Kentucky warbler (kw)	*Oporonis formosus*
Hooded warbler (hw)	*Wilsonia citrina*
Canada warbler (ca)	*W. canadensis*
American redstart (ar)	*Setophaga ruticilla*
Scarlet tanager (st)	*Piranga olivacea*
Cardinal (cl)	*Cardinalis cardinalis*
Rose-breasted grosbeak (rg)	*Pheucticus ludovicianus*
Indigo bunting (ib)	*Passerina cyanea*
American goldfinch (gf)	*Spinus tristus*
Rufous-sided towhee (rt)	*Pipilo erythropthalmus*
Field sparrow (fs)	*Spizella pusilla*
Song sparrow (ss)	*Melospiza melodia*

Plants

Red maple	*Acer rubrum*
Sugar maple	*A. saccharum*
Black birch	*Betula lenta*
American beech	*Fagus grandifolia*
Yellow poplar	*Liriodendron tulipfera*
Norway spruce	*Picea abies*
Pin cherry	*Prunus pensylvanica*
Black cherry	*P. serotina*
Chestnut oak	*Quercus prinus*
Red oak	*Q. rubra*
Staghorn sumac	*Rhus typhina*
Blackberry	*Rubus* spp.
Sassafras	*Sassafras albidum*
Greenbriar	*Smilax* spp.

DISCUSSION

BARRY NOON: Did your principal components analysis give you any additional insights into the species-habitat associations that were not apparent from a simple list of species by habitat type?

BRIAN MAURER: Yes, the PCA helped to identify specific relationships between bird species and habitat variables. For example, both chestnut-sided warblers and common yellowthroats were found on three areas. The PCA showed that yellowthroats were more strongly associated with variables dealing with the abundance and height of herbaceous vegetation, while chestnut-sided warblers were not. These types of relationships are not apparent by simply examining species lists. In the example just given, since both species would appear on lists for the same habitats there would be no way to further differentiate between their specific habitat requirements, other than drawing speculative conclusions from the life history literature.

KEN MORRISON: Why did you use the matrix procedure of SAS rather than PROC FACTOR with METHOD=PRINT to obtain your principal components?

BRIAN MAURER: It is easier to get the factor scores from PROC MATRIX, because you do not need to call an additional procedure. Also, the researcher can easily modify a PROC MATRIX program to fit the particular needs of the data.

PRINCIPAL COMPONENTS ANALYSIS OF DEER HARVEST–LAND USE RELATIONSHIPS IN MASSACHUSETTS[1]

Philip J. Sczerzenie[2]

Abstract.--Relationships of deer harvests with land use and forest cover types in Massachusetts' 351 townships in 1951 and 1971 were investigated using principal components (PC) techniques. PC analysis and PC regression methods are described and their value in reducing the dimensionality of the land-use and forest-type data is emphasized. Components on softwood vs. urban land, stand-age and hardwoods + farmland accounted for over 40% of the X data variability. Increasing softwood composition, decreasing age, and increased association of hardwoods and farmlands were significant positive effects when related to deer harvest levels. PC regression, under well-defined criteria for component deletion, allowed estimation of effects in the original beta-space with reduced variances on those effects while maintaining the statistical integrity of the data sets.

Key words: Forest types; land use; multiple regression; principal components; white-tailed deer.

INTRODUCTION

Massachusetts' legal deer harvests began in 1910 under supervision of the state's Division of Fisheries and Wildlife. Harvest levels increased, except during depression and war years, to a record take of 4,887 deer in 1958. Harvests declined precipitously after 1958, until in 1966 mandatory deer checking, and in 1967 anterless deer permit systems, were instituted.

Two concurrent factors appeared to have caused the decline in harvests. First, either-sex hunting from 1910 to 1966 resulted in an overharvest of does, so the reproductive portion of the herd was unable to replenish itself. Second, farm abandonment and secondary succession that led to buildup of the Massachusetts herds in the late 1800's no longer provided enough productive habitat. Instead, a decline in forage and cover was occurring due to urbanization and forest succession. The antlerless permit system was established to remedy the former problem, and while it was successful in limiting doe take and increasing buck harvests (McDonough and Pottie 1979), it had no effect on the second problem.

The present study was undertaken to quantify effects of different land uses and forest types on deer harvests so that alternative approaches to habitat management could allocate management effort optimally. The 20-year period between samples would tend to strengthen conclusions drawn on the basis of effects that remained the same.

DATA DESCRIPTION

The dependent variable, deer harvest, was the mean 5-year kill in each of 351 townships in Massachusetts from 1949-53 and 1969-73. As recommended by Labisky et al. (1964), kill was transformed using $\log_{10}(1 + \text{kill/mi}^2)$. Deer harvest averages centered on the years 1951 and 1971 to coincide with land-use surveys of the state based on aerial photographs (MacConnell 1975). Aerial photos were land-use typed to approximately 3.5 acres; this information was transferred to topographic sheets; and the area of each of 104 types computed and recorded for each township.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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I used 35 types as independent variables: abandoned fields (AF), pasture (PS), urban land (UL), and 32 forest types (table 1). Acreage of each type was transformed to arcsin square root percent (Steel and Torrie 1960:158). Total acreage of the 35 types was 4,463,360 in 1951 and 4,480,327 in 1971 representing 85.9% and 86.2% of the state's total surface area of 5.2 million acres in respective years.

PRINCIPAL COMPONENT ANALYSIS

Method

Principal component analysis (PCA) has been used by ecologists as one of a number of multivariate techniques to describe habitat preferences of various species of North American breeding birds (James 1971, Smith 1977) and to describe site differences in relation to vegetation communities (Austin 1968, Page 1976).

PCA is helpful because it reduces the dimensionality of a data set, such as an array of environmental variables assumed to influence the species under consideration. A more parsimonious description of habitat influence is possible, therefore, assuming the principal components have some reasonable biological interpretation.

The original data (X), expressed as a matrix of simple correlations (by standardizing $\underline{X}$ and premultiplying by $\underline{X}'$), is transformed into a matrix of principal component scores, $\underline{z}_i$, (regressors in PC regression). This procedure is accomplished by creating a set of eigenvectors, $\underline{a}_i$, and eigenvalues, λ_i.

Each $\underline{a}_i$ is a linear combination of loadings between -1 and +1 on each X_i, constructed so that, in sequence (i=1,2,...,k), the maximum possible amount of variability in the X data is accounted for, with the stipulation that each eigenvector be orthogonal with every other $\underline{a}_i$ ($\underline{a}_i' \cdot \underline{a}_j = 0$).

Each eigenvalue, λ_i, represents the portion of variation explained by its corresponding eigenvector. The following equations apply:

$$\underline{X}\,\underline{a}_i = \underline{z}_i \qquad (1)$$

$$\underline{z}'_i \cdot \underline{z}_i = \lambda_i = \underline{a}'_i\,\underline{X}'\underline{X}\,\underline{a}_i \qquad (2)$$

and the resultant matrix of orthogonal eigenvalues is

$$\begin{bmatrix} \lambda_1 & & & & & \\ & \lambda_2 & & & & \\ & & \lambda_3 & & & \\ & & & \cdot & & \\ & & & & \cdot & \\ & & & & & \cdot \\ & & & & & & \lambda_k \end{bmatrix}$$

When based on the correlation matrix ($\underline{X}'\underline{X}$), $\Sigma\lambda_i = k$, where k is the number of independent (X) variables.

Table 1. Classification of 32 forest types used as independent variables (MacConnell 1973).

Forest composition:
H: hardwoods
S: softwoods
HS: hardwood dominant mixed forest
SH: softwood dominant mixed forest

Forest height classes:
1: one to 20 feet
2: 21 to 40 feet
3: 41 to 60 feet
4: 61 to 80 feet
6: uneven heights (3 or more classes present)

Crown closure classes:[1]
A: 81 to 100% crown closure
B: 30 to 80% crown closure

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[1] Height classes 1 and 6 have no crown closure associated.

Table 2. Eigenvalues and cumulative porportion of X variation of 1951 and 1971 data on 35 land uses.

1951

Eigenvalues

7.98896	4.16814	3.29646	2.63986	1.66862	1.41153
1.35130	1.16983	1.06800	0.84554	0.82070	0.73461
0.69440	0.65197	0.62429	0.59965	0.52160	0.49797
0.45877	0.40060	0.36848	0.35173	0.34111	0.29181
0.27749	0.25885	0.22551	0.21778	0.19392	0.17896
0.16296	0.16006	0.14834	0.11799	0.09221	

Cumulative proportion of total variance of independent variable

0.22826	0.34735	0.44153	0.51695	0.56463	0.60496
0.64357	0.67699	0.70751	0.73166	0.75511	0.77610
0.79594	0.81457	0.83241	0.84954	0.86444	0.87867
0.89178	0.90322	0.91375	0.92380	0.93355	0.94188
0.94981	0.95721	0.96365	0.96987	0.95741	0.98053
0.98518	0.98976	0.99399	0.99737	1.00000	

1971

Eigenvalues

6.82717	4.99291	4.24402	2.84598	2.43800	1.39437
1.24683	1.07258	0.97177	0.79921	0.75289	0.65541
0.56755	0.51426	0.50080	0.46745	0.42616	0.41565
0.39114	0.36751	0.31664	0.30569	0.28716	0.28383
0.27362	0.23534	0.22413	0.20672	0.17137	0.16534
0.15844	0.14815	0.12635	0.11795	0.08863	

Cumulative portion of total variance of independent variable

0.19503	0.33679	0.45895	0.54026	0.60992	0.64976
0.68538	0.71602	0.74379	0.76662	0.78813	0.80686
0.82308	0.83777	0.85208	0.86543	0.87761	0.88949
0.90066	0.91116	0.92021	0.92824	0.93715	0.94526
0.93507	0.95980	0.96620	0.97211	0.97700	0.98173
0.98625	0.99049	0.99410	0.99747	1.00000	

The first few principal components normally account for the bulk of X variability while the last few explain a negligible portion and can, in theory, be disregarded. This reduces the dimensionality of X to z_i, less than k, and, if z_i can be given some interpretation (usually by inspection of eigenvector loadings), a theory about the underlying structure of X can be expounded. With respect to a dependent variable, the relationship between Y and each z_i may be examined, in many cases graphically, to determine how the underlying X structure affects the species of interest. For a more complete treatment of principal component analysis the reader may consult Johnston (1972) or Nichols (1977).

Results

Table 2 lists eigenvalues of the 1951 and 1971 X data (land uses and forest types) in order of importance and the cumulative proportion of total X variance explained by successive eigenvalues. In both cases, the first four eigenvalues account for more than half the variability, leaving the remaining 31 components to explain less than 50%. Figure 1 illustrates the striking similarities between eigenvectors a_1 each year, eigenvectors a_2 each year, and a_3 in 1951 and a_4 in 1971. Each pair of eigenvectors measures the same relationship in X in both years although figure 1A and 1C are mirror images due to pecularities in computation of a_i.

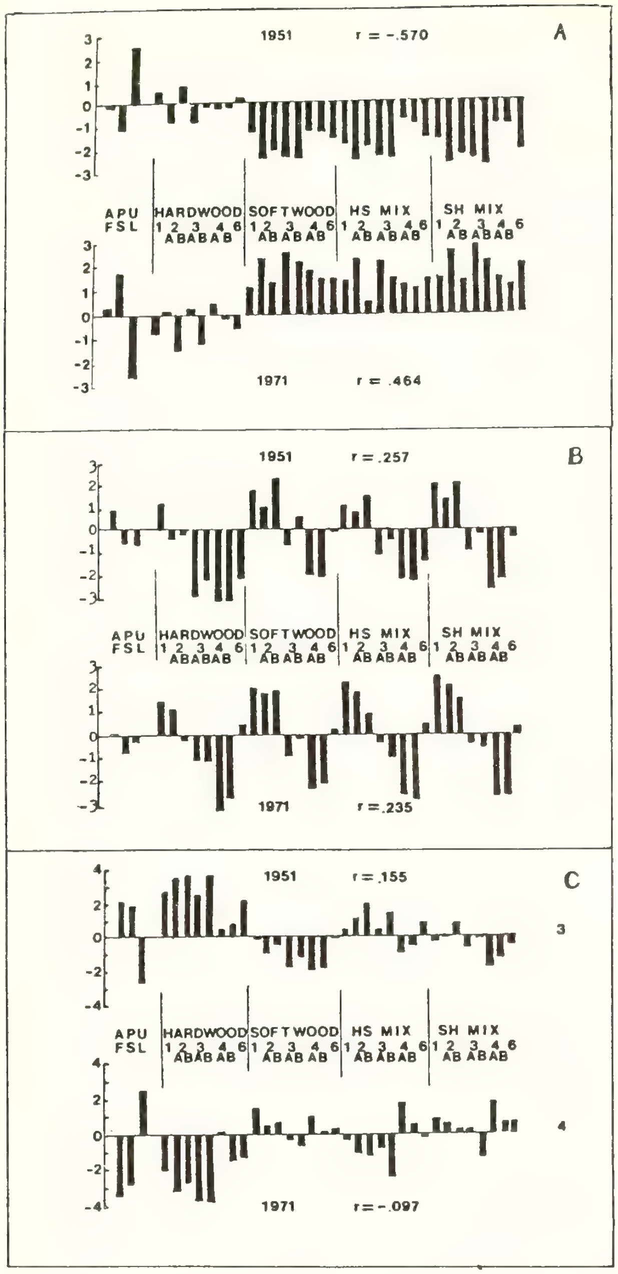

Figure 1. Eigenvectors of 35 Massachusetts land types: (A) eigenvectors $\underline{a}_1$, (B) eigenvectors $\underline{a}_2$, (C) eigenvectors $\underline{a}_3$,$\underline{a}_4$.

All forests with a softwood component have relatively heavy loadings in $\underline{a}_1$ while urban land is weighted in the opposite direction. This can be termed the softwood vs. urban land (SUL) effect. It accounts for about 20% of $\underline{X}$ variability in each year. The second eigenvector is loaded positively for young forest of all types, less positively and eventually negatively for stands of intermediate age, and negatively for older age forest stands. This effect of stand age (STA) remains the same over the 20-year sampling period. Eigenvectors $\underline{a}_3$ of 1951 and $\underline{a}_4$ of 1971 can be described as the hardwood/farmland (HF) effect since they are loaded for hardwood forest types and AF and PS in both years.

Three corresponding pairs of eigenvectors; $\underline{a}_1$, $\underline{a}_2$, and $\underline{a}_3$ of 1951 and a_1, $\underline{a}_2$, and $\underline{a}_4$ of 1971; account for 44 and 42 percent of $\underline{X}$ variability respectively, therefore, the dimensionality of land-use and forest type data has been reduced, to a great extent, to information on three independent axes of variability that have clear structures.

Eigenvectors act on $\underline{X}$ to form principal component scores, $\underline{z}_i$, as follows. Each township has a given percentage composition of the 35 land-use types that constitute, when transformed, the observations X_1, X_2,...,X_k for the township in that year. Each X_i is multiplied by the corresponding eigenvector element and the products summed to form z_i for the township according to equation (1). If a township has, for example, large percentages of older hardwoods and urban land in 1971, its score for z_1 would be negative, for z_2 negative and for z_4 positive.

Relationship with Deer Harvest

Relationships between principal axes of land-use and forest-type variation and corresponding township deer kill levels are summarized in table 3. Component 1 in each year has the highest eigenvalue, explains the highest percentage of $\underline{X}$ variation, and has the highest simple correlation with deer harvest. Because the $\underline{a}_1$'s are mirror images their corresponding r's are of opposite sign. One can conclude townships with low amounts of urban land and higher acreage of softwoods are more productive of deer. Component 2 in each year explains less $\underline{X}$ variability and has a lower, positive correlation with deer harvest, thus, stand-age is an important determinant of a township's productivity for deer. Those with older stands, in general, have fewer deer harvested.

The third PC effect, hardwood/farmland, has a relatively low correlation with deer harvest and, therefore, although townships with more hardwoods generally have higher harvests, one would tend to manage for softwoods or mixed forests rather than hardwoods since the latter is a much stronger relationship and appears to contradict the former finding. The combination of hardwoods and farmland, on the other hand, may serve as an indication of the relative lack of urbanization in a township and, in this respect, would reasonably be associated with higher deer harvests.

Table 3. Comparison of three important principal components of 1951 and 1971 data on three land-use and 32 forest types.

Year	Component	Eigenvalue	$\underline{X}$ Variation explained (%)	r	b[1]
1951	1	7.989	22.8	-0.570	-0.148
1971	1	6.826	19.5	0.464	0.133
1951	2	4.168	11.9	0.257	0.092
1971	2	4.993	14.3	0.235	0.079
1951	3	3.296	9.4	0.155	0.063
1971	4	2.846	8.1	-0.097	-0.043

[1] Prinicpal component beta coefficients, $P < 0.01$.

PRINCIPAL COMPONENTS REGRESSION

Method

Least Squares Model

The preceding PC analysis was done as an intermediate stage in what many researchers consider the primary purpose of multivariate analysis, estimation of coefficients on the original variable set. Thus, the value of principal components lies in their usefulness in solving the general linear model:

$$Y_j = B_o + B_1 X_{1j} + B_2 X_{2j} + \ldots + B_k X_{kj} + u_j \qquad (3)$$

where Y_j are observations on the dependent variable, ($j=1,2,\ldots,n$) B_o is the intercept, B_i is the effect of the i^{th} independent variable on Y, ($i=1,2,\ldots,k$), and u_j is a randomly distributed error or disturbance term. In matrix notation (3) becomes

$$\underline{Y} = \underline{X}\ \underline{B} + \underline{e} \qquad (4)$$

where $\underline{Y}$ is an n x 1 vector of dependent variable observations, $\underline{X}$ is an n x k matrix of independent variable observations, $\underline{B}$ is a k x 1 vector of coefficients on $\underline{X}$, and $\underline{e}$ is a residual term (substituted for $\underline{u}$) that is the difference between $\underline{Y}$ observed and $\underline{Y}$ predicted using our estimate of $\underline{B}$.

Using the matrix $\underline{A}$ of k eigenvectors derived from the matrix $\underline{X'X}$ of correlations, we form the n x k matrix of z scores $\underline{Z}$ by the k x 1 vector $\underline{d}$ of coefficients on the scores as

$$\underline{Y} = \underline{XA'A}\ \underline{B} + \underline{e} = \underline{XAd} + \underline{e} = \underline{Zd} + \underline{e} \qquad (5)$$

The vector $\underline{d}$ of PC coefficients is easily solved for

$$\underline{d} = (\underline{Z}'\underline{Z})^{-1}\ \underline{Z}'\underline{Y} + (\underline{Z}'\underline{Z})^{-1}\underline{Z}'e \qquad (6)$$

since

$$\underline{Z}'\underline{Z}^{-1} = \begin{bmatrix} 1/\lambda_1 & & & & \\ & 1/\lambda_2 & & & \\ & & \cdot & & \\ & & & \cdot & \\ & & & & \cdot \\ & & & & 1/\lambda_k \end{bmatrix}$$

The second term on the right in (6) is zero. This leads to the ordinary least squares (OLS) solution when $\underline{d}$ is transformed back to the original beta-space using $\underline{B} = \underline{Ad}$.

Component Deletion

The PC regression (PCR) solution, therefore, calls for deletion of one or more components to rid the data structure of "noise" that provides little in the form of information about $\underline{X}$ variation (recall cumulative proportion of variability from table 2) but adds considerably to variance about $\underline{B}$.

The data structure is partitioned as:

$$\underline{Y} = \underline{XA}_1\ \underline{d}_1 + \underline{XA}_2\underline{d}_2 + \underline{e} = \underline{Z}_1\underline{d}_1 + \underline{Z}_2\underline{d}_2 + \underline{e} \qquad (7)$$

and deletion of the second portion is required. This is equivalent to the restriction $\underline{XA}_2\underline{d}_2 = 0$ (Fomby and Hill 1978). If the restriction is true, the estimator remains unbiased.

Test of the restriction is as follows:

$$u = \frac{(SSR_{res} - SSR_{ols})/ J}{SSR_{ols} / n\text{-}k} \qquad (8)$$

where SSR_{res} and SSR_{ols} are residual sums of squares on the restricted and unrestricted (OLS) models respectively, J is the number of restrictions (deleted components) and n and k are as defined above. Because this is a test of the truth of $\underline{XA}_2\underline{d}_2 = 0$, i.e., $\underline{A}_2 = 0$, the test statistic u is compared with a centrally distributed F, a classical F-test.

If one is willing to accept some bias for further reducing variances on $\underline{B}$, a mean square error (MSE) criterion can be used minimizing $\Sigma(\text{var} + \text{bias}^2)$. This uses the same test statistic u but now comparison is with a non-central F distribution (Goodnight and Wallace 1972). Should further component deletion be desired, some eigenvalue size criterion might be employed, however, statistical properties of the resultant estimator, as in stepwise regression (Freund 1974) will be unknown.

Table 4. Results of the 1951 analyses under OLS, classical F, and MSE criteria of deer kill versus 35 land-use types defined in table 1.

Land-use type	$\underline{b}$ OLS	$\underline{b}$ Cl "F"	$\underline{b}$ MSE
AF	1.75 **	1.81 **	1.70 **
PS	-.269 **	-2.56 **	-2.43 **
UL	-.378 **	-3.60 **	-3.45 **
H2A	-0.37 ns	-0.08 ns	1.14 **
H2B	-3.96 **	-3.60 **	-3.59 **
H3A	-1.95 ns	-0.36 ns	-1.63 **
H4A	-3.80 **	-3.64 **	-3.05 *
S4A	9.31 *	9.27 *	9.12 *
HS1	-2.68 **	-2.18 **	-1.94 **
HS2A	-2.23 *	-3.22 **	-2.97 **
HS3A	-0.39 ns	0.91 ns	2.17 **
SH2A	1.12 ns	2.18 **	0.66 ns

* $P < 0.05$, ** $P < 0.01$, ns = nonsignificant

Results

The data sets for 1951 and 1971 were analyzed by principal component regression (tables 4 and 5). In the analysis of 1951 data, one component was deleted under the classical F criterion and one additional component deleted under the MSE criterion. For the 1971 data all components were retained under the classical F criterion, so the OLS model is the only unbiased estimator of $\underline{B}$ in terms of the specified model assumptions. Under the MSE criterion a single component was deleted.

Coefficients produced in the study are consistent from year to year and within year-period under OLS and both deletion criteria. Those effects found significant in both years, PS, UL, H2A, H3A, HS2A, and HS3A remained of the same sign and magnitude. The close agreement over the 20-year period and under deletion criteria within each year lead me to conclude that real relationships have been estimated.

Clearly, results show urban land as a significant negative effect in 1951 and 1971; this was to be expected. Other significant negative effects for both years were pasture, cutover hardwoods (H2B), older hardwoods (H3A), and a young mixed type (HS2A).

Table 5. Results of the 1971 analyses under OLS and MSE criteria of deer kill versus 35 land-use types defined in table 1.

Land-use type	$\underline{b}$ OLS	$\underline{b}$ MSE
PS	-2.04 **	-1.85 *
UL	-4.63 **	-4.26 **
H1	2.01 *	2.41 **
H2A	1.72 *	2.27 **
H2B	-3.87 **	-4.04 **
H3A	-1.72 **	-1.83 **
S1	-4.09 *	-4.03 *
S2A	4.30 **	4.84 **
S3A	-2.64 *	-2.18 *
S3B	3.65 *	3.87 *
HS2A	-1.62 ns	-2.52 *
HS3A	-0.33 ns	0.88 **
SH3A	-2.69 ns	-2.49 **

* $P < 0.05$, ** $P < 0.01$, ns = nonsignificant

Significant positive effects in both periods were young, dense-canopy hardwoods (H2A) an older, dense-canopy mixed forest (HS3A). Softwood types were found significantly positive in both periods but specific types were also identified as negative effects in 1971.

Age, canopy-closure and softwood mixture of hardwood and hardwood-dominant mixed forest types appear to be governing factors in terms of individual type effects on deer harvests. With softwood composition, this accounts for much of forest type effect on harvests. Young, dense hardwood stands are used by deer as a major source of browse while some of the more open softwood stands may function both as winter cover and feeding areas.

Those types that were negative (H2B, H3A, H4A, HS1, HS2A) may provide neither enough food nor enough escape cover in limited areas to be acceptable to deer. The negative softwood types (S3A, SH3A) because of their year-round dense canopies, likely provide little food or cover at all. Old softwood types that were positive effects (S3B, S4A) may function primarily as wintering sites with enough light penetration through or underneath the canopy to support an understory.

It is possible, therefore, to explain why the land-use types investigated had their calculated effects on deer harvests, although this may be viewed as a simplistic causal assumption. There are, of course, many effects of different land-use and forest types, both direct and indirect, that enter into the investigated relationships. Nevertheless, quantification of these general relationships may eventually lead to better definition of specific hypotheses about impacts of land-uses and forest composition.

CONCLUSIONS

Principal component analysis has shown an underlying structure in land-use and forest type composition in Massachusetts that is consistent over a 20-year period. Relationships between these axes of variability and deer harvest are also consistent and are capable of reasonable biological interpretation.

Principal component regression has allowed elucidation of individual type effects on deer harvest by reducing variances on B̲ under criteria that produce known statistical properties. This is in direct contrast to data-dredging techniques, such as stepwise regression, that eliminate independent variables through mechanical manipulation and that leave B̲ estimators that are unreliable, at best, because their statistical properties are not known. PCA and PCR are therefore seen as valuable multivariate analytical tools for the ecological investigator.

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AN APPLICATION OF FACTOR ANALYSIS IN AN AQUATIC HABITAT STUDY[1]

T.J. Harshbarger[2], and H. Bhattacharyya[3]

Abstract.--In five small, high-gradient trout streams in western North Carolina, 18 cover variables were related to standing crop biomass of wild brook trout (Salvelinus fontinalis), rainbow trout (Salmo gairdneri) and brown trout (Salmo trutta) in randomly selected stream sections. Factor analysis of the data set showed that only a small number of factors or variables was needed to explain relations between variables in the observed set. Key cover factors were area in debris; turbulent water; vegetation, both in and over stream; and overhanging banks. Resolutions obtained were used in stepwise regressions to explore relationships between standing crop of trout and age of fish. Regressions containing factors as independent variables explained less variation in fish standing crop than did regressions containing equal numbers of original habitat attributes as independent variables.

Key words: Aquatic habitat; cover; factor analysis; multivariate analysis; regression analysis; stream fish; trout.

INTRODUCTION

The presence of a self-sustaining population of fish usually indicates compatibility between the aquatic envrionment and the ecological requirements of the fish. Wild trout are excellent indicators of current environmental conditions and their population density in streams reflects their level of compatibility with a highly integrated chemical, physical and biological situation. However, simply realizing that the trout population reflects its envrionment is not particularly informative to the resource manager. Explicit relationships between species and their environments are needed to assess the actual and potential capabilities of the habitat.

Functional and correlative approaches have been used to study factors influencing the distribution and abundance of a species. The functional approach is used when factors are known to influence certain attributes of the species. Correlative procedures are best suited for exploratory studies, where the relationship between a species and its environment are unknown. This procedure provides little information about causality, but helps the researcher to make inference for rigorous testing. Many variables can potentially influence the distribution and density of wild trout in a stream. Often the choice of parameters to measure and analyze is difficult because environmental variables in lotic waters are typically correlated and confounded with one another (Reid 1961).

Attempts to correlate single and multiple variables to trout populations in streams have met with varying degrees of success. Boussu (1954), Saunders and Smith (1962), and Wickham (1967) investigated the relationship of a trout population to cover. In two studies (Schuck 1943, Hunt 1969), water depth strongly influenced trout densities in streams, and current velocity was similarly implicated in another study (Lewis 1969). Few investigators, notably Lewis (1969), Stewart (1970), Platts (1974), and Binns and Eiserman (1979), have studied the simultaneous effect of several environmental variables on stream trout populations using multiple regression and correlation analysis.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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The present study was designed to look at the relationships between various habitat parameters and trout. Factor analysis was used to delineate and examine a group of environmental variables that seemed important to trout, those providing cover or shelter. Regression analysis was used to examine relationships between the environmental factors produced and trout.

STUDY SITES AND METHODS

We selected five small, high-gradient trout streams in western North Carolina. In each, we inventoried and measured 18 variables providing fish cover, in 20 randomly selected 30m stream sections. Each section was surveyed along line transects established every 3m across the stream, perpendicular to its center line. All physical structures providing shelter or concealment for trout were located and their cross-sectional areas parallel to the air-water interface recorded. Structures included rocks or ledges which afforded cover to fish, undercut banks, aquatic vegetation, and logs and brush in the stream. Other cover situations such as water with sufficient surface turbulance to prevent visibility of the stream bottom were also measured and recorded.

Brush and loosely compacted debris in the stream and streamside vegetation overhanging the water surface were estimated ocularly. Cover afforded by brush and debris was recorded as the surface occupied by solid material and expressed as a percentage of the water surface it covered. Cover provided by overhanging bank vegetation was expressed in two variables: as the percentage of stream covered by vegetation between the water surface and 1.0m above, and the percentage between 1.0m and 2.0m above the surface.

Standing crop biomass of wild trout was estimated by depletion analysis electrofishing. All fish were weighed, measured, and returned to the midpoint of the section under study.

Factor Analysis

Starting with the observed correlation matrix on the 18 cover variables, we used SAS FACTOR programs for principal axis, maximum likelihood, and iterated principal axis factoring (SAS 1979). Using the principal axis method and keeping only those factors corresponding to eigenvalues greater than one, six factors were retained. To make the factors more conceptually meaningful, several rotational methods were used, including varimax, quartimax, equimax and promax (oblique) procedures (SAS 1979).

All factor and rotation procedures used on the 18 cover variables produced essentially the same information about underlying structure. However, the iterated principal axis and oblique rotational procedures are intuitively appealing. These procedures address communalities directly and recognize that some factors may very likely be correlated. As such only the interated principal axis solution using an oblique rotation of the cover related factors will be presented in this paper.

Regression Analysis

Relationships between standing crop of trout and the factors obtained from oblique rotation of the iterated principal axis solution were explored using SAS STEPWISE regression procedures and the maximum R^2 improvement technique developed by Goodnight (SAS 1979). Relationships between the habitat variables themselves and standing crop of trout were similarly explored to determine if factors entered the stepwise model in about the same order as the variable they contained. Coefficients of determination were compared to assess performance of models containing factors and variables.

RESULTS

The six factors combined the 18 cover variables into groups which generally reflected meaningful patterns in relation to the stream environment. Factors were named after the variable or variables producing greatest correlation. Factor loadings for the variables are shown in table 1. Factors had zero or close to zero projections on most variables, very few immediate loadings, and two or three high associations.

Factor 1 is a measure of debris with high loadings for number of logs and the surface areas, parallel to the stream, in logs and in brush. Factor 2 is a measure of side stream cover and is strongly negatively correlated with area in and percent cover of vegetation trailing in the water surface. The third factor expresses the percentages of cover provided by overstream vegetation 0-1m and 1-2m above the stream. Factor 4 is highly correlated with area in turbulent water and to a lesser degree with the number of units of turbulent water. This factor is also correlated with total cover and can be considered a general cover factor. Rock area and number load heavily on factor 5, and the sixth factor is highly correlated with area in overstream vegetation in the 1- to 2-m zone.

Factor values for each of the 100 stream section observations were obtained from the scoring coefficient matrix. Trout, regardless of

Table 1. Variables associated with cover factors.

Variables	Factor loadings					
	1	2	3	4	5	6
Ledge area (1)	0.063	0.241	0.030	0.400	-0.288	0.106
Rock						
Number (2)	-0.075	-0.047	-0.009	-0.096	0.850	0.214
Area (3)	0.099	0.194	0.114	0.109	0.646	-0.191
Turbulent water						
Number (4)	-0.108	0.304	-0.075	0.491	0.007	0.156
Area (5)	-0.244	-0.054	-0.059	0.936	-0.115	-0.014
Logs						
Number (6)	0.913	-0.049	-0.007	-0.108	-0.146	-0.003
Area (7)	0.969	0.003	-0.060	-0.089	-0.019	0.020
Bank area (8)	0.080	-0.539	-0.039	-0.125	-0.119	-0.080
Other area (9)	0.045	0.002	0.345	-0.051	0.112	-0.090
Brush						
% Cover (10)	0.102	-0.150	0.282	0.062	0.033	-0.012
Area (11)	0.824	0.076	0.067	-0.006	0.084	0.076
Side-stream vegetation						
% Cover (12)	-0.116	-0.772	0.048	-0.087	0.082	0.198
Area (13)	0.001	-0.712	0.006	0.012	0.011	0.015
Over-stream vegetation (0-1m)						
% Cover (14)	-0.045	-0.042	0.896	0.034	-0.109	-0.201
Area (15)	0.174	0.217	0.111	0.231	-0.333	0.363
Over-stream vegetation (1-2m)						
% Cover (16)	-0.032	0.089	0.844	-0.110	0.039	0.293
Area (17)	0.048	-0.050	-0.062	0.046	0.094	0.999
Total cover area (18)	0.365	-0.105	0.062	0.775	0.225	-0.076

species, in each stream section were segregated into the four age classes represented in each of the five streams under study. The relationship between factor values and trout standing crop for each age group was examined using the stepwise maximum R^2 regression technique. Likewise, the relationship between the original 18 cover attributes and trout standing crop was similarly examined.

The coefficient of determination (R^2) corresponding to the six factors was lower than that corresponding to the original 18 variables for each age class of fish (table 2). Further, the best one-attribute, two-attribute, etc., models obtained by the stepwise procedure also produced higher R^2 values when the original variables were used than when the deduced factors were used. Six-factor models produced coefficients (R^2) which ranged from 0.09 for the standing crop of the young-of-the-year trout to 0.53 for trout in age group II. Regressions on the original variables produced coefficients between 0.31 and 0.71 for 18 variable models and 0.26 and 0.66 for models containing six variables.

For young-of-the-year trout a single variable, rock area, produced an R^2 value (0.10) equivalent to that obtained from the model containing all six factors. In age group I, two habitat variables, numbers of rocks and total cover, produced a coefficient (0.18) as large as the six-factor model. A coefficient similar to that produced by the six-factor model was obtained for trout in age group II with three variables (R^2=0.56); number of rocks, percent cover provided

Table 2. Order in which the habitat attributes shown in table 1 entered stepwise regressions and the coefficient of determination they produced for each age group of trout.

Age group	Step 1 Attributes (R^2)	Step 2 Attributes (R^2)	Step 3 Attributes (R^2)	Step 4 Attributes (R^2)	Step 5 Attributes (R^2)	Step 6 Attributes (R^2)
Group 0						
Factors	6 (0.03)	4,6 (0.05)	3,4,6 (0.07)	2,3,4,6 (0.08)	1,2,3,4,6 (0.09)	1,2,3,4,5,6 (0.09)
Variables	3 (0.10)	2,3 (0.16)	2,3,12 (0.23)	3,12,15,27 (0.29)	2,3,12 15,17 (0.31)	2,3,10,12, 15,17 (0.32)
Group I						
Factors	5 (0.08)	4,5 (0.12)	1,4,5 (0.14)	1,2,4,5 (0.15)	1,2,3,4,5 (0.15)	1,2,3,4,5,6 (0.15)
Variables	2 (0.14)	2,18 (0.18)	1,2,10 (0.21)	1,2,3,10 (0.23)	1,2,3,4,12 (0.25)	1,2,3,4,10,12 (0.26)
Group II						
Factors	6 (0.17)	5,6 (0.40)	4,5,6 (0.46)	2,4,5,6 (0.49)	1,2,4,5,6 (0.52)	1,2,3,4,5,6 (0.53)
Variables	2 (0.31	2,3 (0.44)	2,10,17 (0.55)	2,10,15,17 (0.61)	2,10,12,15,17 (0.64)	2,10,12,15, 17,18 (0.66)
Group III						
Factors	6 (0.16)	5,6 (0.27)	2,5,6 (0.31)	1,2,5,6 (0.35)	1,2,4,5,6 (0.36)	1,2,3,4,5,6 (0.37)
Variables	17 (0.23)	15,17 (0.29)	12,15,17 (0.35)	4,12,15,17 (0.38)	2,4,12,15,17 (0.40)	2,4,10,12, 15,17 (0.42)

by instream brush, and area in overstream cover between 1 and 2 m; and for trout in age group III with four variables (R^2=0.34); number of pockets of turbulent water, percent cover of side-stream vegetation, area in overstream cover to 1 m, and area in overstream cover to 2 m.

Factor 5 (rocks) and factor 6 (area in overstream cover 2 m and above) and their equivalent habitat attributes were, in most instances, the first parameters to enter stepwise regressions containing factors or variables. Factor 2 (overstream cover) and factor 4 (general cover) entered models intermediately, and factor 1 (debris) and 3 (percent overstream cover) entered models last. Area in and percent cover provided by side-stream vegetation consistently entered models intermediately. Other habitat attributes either entered models intermediately or late in the stepwise procedure.

DISCUSSION

Factor analysis was useful in defining the underlying structure of the cover portion of the habitat for trout. Although 18 variables were singled out and measured, cover consists essentially of a six-dimensional space characterized by six factors: debris, side-stream cover, percent of overstream vegetation, turbulent water, rock area, and area of overstream vegetation in the 1- to 2-m zone.

In examining the relationships between standing crop of fish and the habitat attributes by stepwise regression methods, a higher coefficient of determination (R^2) was obtained by using the 18 original variables than by using the six derived factors. Moreover, it was found that the best one-attribute, two-attribute, etc., models also resulted in higher R^2 values when original variables were used. This indicates that when the original variable measurements are available, there is no reason to form regression models based on derived factors. With the exception of 2-year-old trout, no R^2 value between trout and the set of variables exceeded 0.5, indicating that there is a substantial portion of variability in fish biomass that is not explained by the measured variables and hence also not explained by the derived factors. Part of this variability may be accounted for by water or flow related variables. The results of a combined analysis of water and cover variables will be reported at a later date.

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DISCUSSION

TERRY LARSON: Most papers given here which involved multiple regression analysis used stepwise techniques. Why did you not use an all possible subsets technique like BMDP-9R? This program is not costly to run and will pick up subsets that stepwise techniques miss.

HELEN BHATTACHARYYA: The SAS STEPWISE procedure with MAXR option was used. You are quite right that all possible regression (SAS RSQUARE procedure) may pick out combinations not covered by stepwise. However, STEPWISE/MXR is almost as good (see SAS writeup) and has the advantage of printing all other regression statistics, slope, intercept, mean squares, etc., besides just the R^2 value.

New Approaches to Analysis and Interpretation

BIRD COMMUNITY USE OF RIPARIAN HABITATS: THE IMPORTANCE OF TEMPORAL SCALE IN INTERPRETING DISCRIMINANT ANALYSIS[1]

Jake Rice[2], Robert D. Ohmart[3], and Bertin Anderson[4]

Abstract.--Discriminant functions analyses were used to differentiate habitats used from habitats not used by every bird species in the lower Colorado River riparian areas, during the breeding season. Most of these DFA's produced statistically significant results, but the mean percent of transects correctly classified into the species-present or species-absent groups, across all species, was less than 75%. Patterns of errors of classification were examined and found to be random with regard to vegetation community, foliage structure or avian species.

When we considered a second year's census data, for 18 of 21 species a significant number of errors in predicted occurrences were "corrected" with the new avian distributions. The habitat DFA's were then repeated between the group of transects used both years and those not used both years. Across all species and all seasons, transects could be correctly classified with an accuracy of 89%. We also found biologically meaningful patterns of seasonal variation 1) in habitat selectivity of the avian community, 2) in differences among vegetational communities and 3) of transects with irregular occurrences of the avian species.

Key words: Birds; Colorado River; community ecology; discriminant function analysis; habitat use; riparian; species turnover.

INTRODUCTION

During the past decade there has been a major upswing in the use of multivariate statistics in the study of ecology. In avian studies the uses have been largely to quantitatively describe community structure through various types of ordinations (James 1971, Whitmore 1975, Conner and Adkisson 1977), or to document niche partitioning among groups of species (e.g., Cody 1968, Hespenheide 1971, Whitmore 1977). This predisposition toward each of these goals can be understood, given current areas of emphasis of theory in community organization and evolutionary ecology in general. The relationships among bird species, and between bird species and characteristics of their habitats, have proven reconcilable with theory, and have often even led to enlightening extensions of our understanding of ecological processes.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop. April 23-25, 1980, Burlington, Vt.

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On the other hand, a large number of these studies can be, and often have been, criticized (if rarely in print, frequently in discussions) for taking a very casual attitude toward several aspects of the original data. There are a variety of potential sources of variation that can be reflected in ecological data, and valid, useful, management studies require research designs that take adequate account of these kinds of variability. Specifically, relatively little attention has been given to verifying that the basic data sets on which the multivariate techniques are used: 1) sample the true and complete range of habitats acceptable to species included in an area; 2) cover the within-species variability in habitat use across communities; and 3) cover the season-to-season and year-to-year variation in bird-vegetation relationships, although a few papers considering some of these points can be found (e.g., Smith 1977, Rotenberry 1978, Rotenberry et al. 1979).

A comprehensive understanding of community ecology will require detailed investigation of each of those sources of variation. Additionally, when investigations move from the theoretical realm to the practical, all of these considerations become even more important. If habitat management plans are actually going to be developed and implemented based on the results of sophisticated quantitative studies, it is essential that the findings truly reflect the species-habitat relationships and are not just statistically significant or consistent with one of many diverse theoretical expectations.

As specific examples, the questions of which spatial scale and which temporal scale to sample become of paramount importance. Furthermore, the errors that occur, for example, in the classification step of a discriminant function analysis, are no longer simply inconveniences or embarrassments, but they become real problems affecting the potential success of any habitat management plan. This paper presents discriminant functions investigations into the habitat use patterns of an entire avifauna; looking particularly at what the errors of classification truly represent, at least in our system, and what temporal scale is suitable for bird habitat studies.

Riparian habitats in the desert Southwest are rich ecological oases for many species of birds and mammals. These areas are also subjected to intense competing land and water use demands for agricultural lands, municipal and industrial purposes, river channel and flood control, and recreational use, in addition to their value for wildlife. For several years the Colorado River Project has been quantifying wildlife densities and use of all riparian habitats along the lower Colorado River. We are currently using these data to develop a predictive model of bird-vegetation (and soon mammal-vegetation) relationships within the system. This model will be used by state, federal and private concerns in actual land use decision making and will be a major tool in assessing and planning habitat mitigation in these riparian areas.

Because of the intended use of our findings we had to know not simply how species X and Y differed in habitat preferences in an area, or even what major gradients we could uncover in community structure. Rather, we had to know, out of the complete range of riparian habitats available, which habitat factors determined or allowed the occurrence of each avian species. Our answers had to be valid over the entire year, because management decisions directed toward a single season will nonetheless have year-round ramifications. Correspondingly, our results had to be valid for several years, not for just whatever special conditions reigned for any single year.

METHODS

It required 72 transects of 1600 m or 900 m to census every community present in each stage of development and in the proportion in which each habitat type occurred along the lower Colorado River. Each transect was then censused three times each month using the familiar strip method (Emlen 1971, 1977). On the basis of climatic and demographic patterns, we divided the year into five seasons: Spring (March-April), Summer (May-June-July), Late Summer (August-September), Fall (October-November) and Winter (December-January-February). Censuses within each season were averaged when we calculated bird species occurrences and densities.

Every tree by species within 16 m of each side of each transect was counted. Also foliage density measures at several heights were taken at 50 m intervals along each transect. The vegetation density measures were combined to produce, for each transect, a 12 variable array describing the foliage density at each stratum, the relative species composition (transformed with the ARCSIN square root transformation), and the foliage height diversity of that transect. These variables were all habitat attributes which we believed were both potentially adequate to characterize habitat use by members of the avian community and were realistically manageable from both the standpoints of data analysis and habitat management.

We used discriminant functions analyses to quantify habitat use attributes of each species. For each species, each season, we divided the pool of 72 transects into two groups: those where the species in question was recorded, "Present", and those where the species was not recorded, "Absent". The Present and the Absent groups of transects were then differentiated on the array of habitat measures, to quantify both how different the used and the unused areas were vegetationally, and what attributes of the vegetation characterized the areas used by each species in the community. Actually, for many species (those with widespread distributions and widely differing abundances on different transects), we repeated the analyses using three or even four groups, based on increasing densities. The accuracy of those analyses were comparable to those of the two group discriminations. The multigroup analyses only introduce further complications because of the additional possible axes of discrimination, and they will not be discussed.

RESULTS AND DISCUSSION

Single-year Discriminations

A synopsis of results of discriminant function analyses for the 39 species which were present during the summer is presented in figure 1. The majority of individual species discriminations showed that habitats were significantly different between used and unused areas. However, quite a number were not different statistically; a matter for possible concern. Some of these cases may represent strictly statistical problems, of the sort discussed by Williams (1981), whereas others might represent species truly showing no vegetation differences between used and unused sites.

Rather than go into all possible investigations of sources of statistical artifacts or errors, we had previously decided that results of the classification step of the discriminant function analyses would be most appropriate for our model, and to us it represented the most important measure of the success of the analyses. We knew, for example, that necessary assumptions of homogeneity of variances and covariances between the Present and Absent groups of transects would often be violated by species with either very widespread or restricted occurrences in the riparian vegetation. Such violations would affect the statistical significance of the analyses. However, regardless of the statistical significance of any given discrimination, if we were able to correctly identify areas that were commonly used by a particular species on the basis of vegetation attributes, we felt we would have a useful management tool.

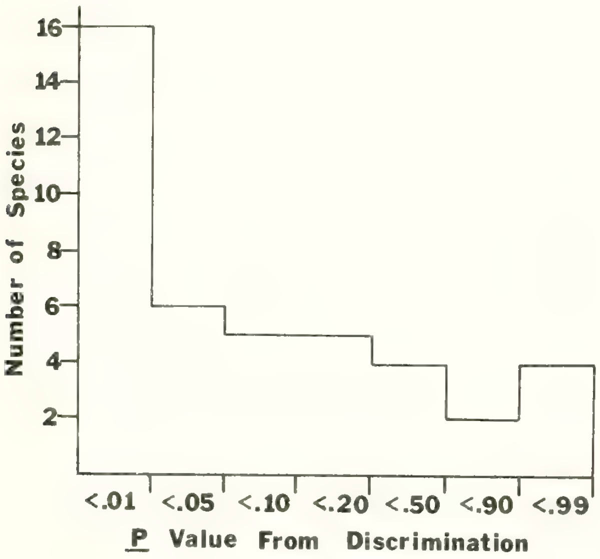

Figure 1. The number of species for which the discriminant analyses of used versus unused habitats reached specific levels of significance. Distribution data were from a single summer.

Table 1. Types of transect classifications possible and their biological significance.

		Status predicted from classification step of the discriminant analyses.	
		PRESENT	ABSENT
Actual status of species on transect	PRESENT	A	B
	ABSENT	C	D

A = Correct prediction of the species presence on the transect

D = Correct prediction of the species absence on the transect

B = Suitable habitat identified as unsuitable for the species

C = Unsuitable habitat identified as suitable for the species

Statistically, the classification step of a discriminant function analysis could produce two different types of errors, illustrated in table 1. From a management standpoint, the two possible types of classification errors are quite different in their importance, and use determines which errors are most serious. To include some unused areas in the used group (C errors, table 1) would be a conservative error for habitat preservation activities. It would lead to preservation of some unsuitable habitats as well as all suitable ones. The other type of error (B errors, table 1) would be more serious; one would reject areas which were, in fact, good habitats for the species in question. Conversely, if one were engaged in management activities to create or modify habitats, the seriousness of the errors would be reversed. To make type B errors would be to develop only some of the range of habitats suitable for a species, whereas to make type C errors would be to spend time and resources developing habitats which would turn out to be unsuitable for the species.

Analysis of Errors

Figure 2 shows the distribution of the percent of correct classifications of transects for the single year discriminant analyses. Although we found few gross failures in the classification steps, there were also correspondingly few species for which we had great success at predicting transect suitability. Rather than continue to use this equivocal tool with data from other seasons, we decided to look in detail at what sorts of errors were occurring, in hope of isolating specific problems of the approach. Possible sources of errors in this study (and correspondingly, other similar studies) included: 1) uneven variability in either the suitability of habitats or the distribution of the species on a scale small enough to affect our findings; 2) inadequate habitat measures, i.e., we had not measured plant community traits important to avian habitat selection; and 3) low habitat selectivity by the bird species, i.e., the used and unused areas truly did not differ. To be tractable, we chose 21 of 39 avian species for detailed investigation, arbitrarily selecting the first 21 species from an alphabetical listing of all the species present.

We looked first at the habitat variability problem; that is, were our discriminations poor because some specific habitats were particularly good or bad at supporting avian species? This is an aspect of the question posed by several ecologists, such Colwell and Futuyma (1971) and Willson (1974); that is, are all equal mensural discontinuities along a resource continuum of equal biological importance?

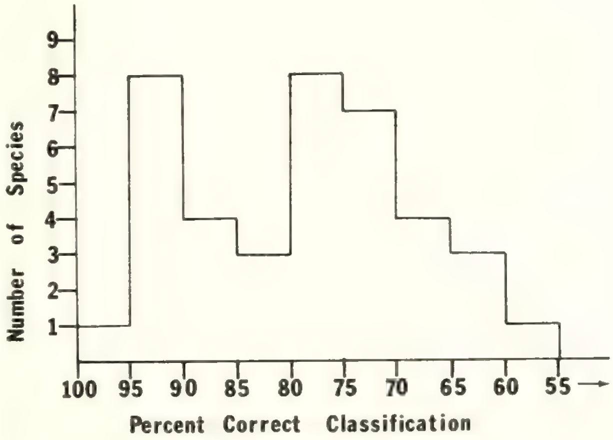

Figure 2. The number of species for which the classification functions of the discriminant analyses were able to correctly identify transects as used or not used at various accuracy rates.

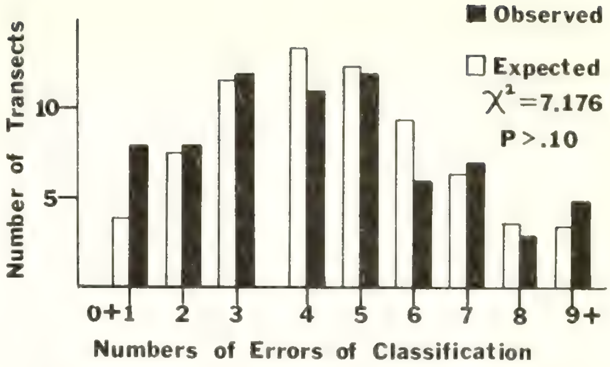

Figure 3. Fit of number of errors of classification of species suitabilities per transect to a Poisson distribution.

We investigated this problem in a simple way. Across the 72 transects there was a mean of 4.64 species misclassified per transect. If these errors were random, we would expect the number of transects with no species misclassified, with one species misclassified, with two species misclassified, and so on, to be distributed as a Poisson (random pattern) with a mean of 4.64. If specific types of habitats were either better or worse than average in terms of their ability to support species, relative to other habitats nearby on the vegetation continua represented by the discriminant functions, the distribution of errors per transect would deviate from the expected values. There was an excellent fit to the predicted distribution (fig. 3). From this we concluded that our error rate was not tied, at least primarily, to differential habitat attractiveness, beyond those differences captured in our vegetation measurements on each transect.

Initially we had intended to use data from subsequent years to test the effectiveness of the model. However, looking at the distributional data from the next year might shed light on the degree of consistency of habitat selection of the species in the avian community. From the classification step, we knew for each species: 1) the number of transects where the species was absent, yet were classified by the analysis as suitable habitat, and 2) the number of transects where the species was present, yet were classified by the analysis as unsuitable habitat. From the occurrence data for the next summer across the same 72 transects, we also determined: 3) the number of transects missing each species in the first year but supporting it in the second; and 4) the number of transects supporting each species in the first year but missing it in the second. All four of these counts can be converted into probabilities simply by dividing by 72 (the number of transects). If errors of classification were true errors with no biological relationship to species occurrences, the product of 1 and 3 and of 2 and 4 would give the expected number of new species occurrences that were "corrections" of previous type C errors and the number of new species absences that were "corrections" of previous type B errors.

We found a surprisingly high rate of species turnover. New appearances occurred on 18% of all possible species-transect combinations, and new absences occurred in 16% of the species-transect combinations. On a species-by-species basis, the predicted number of independent "corrections" due to these species turnovers was usually too low for statistical comparison (commonly one to three expected "correct" new transect appearances or absences per species). However for 18 of the 21 species, the actual number of correct new appearances was greater than the predicted number, and for 16 of 21 species, the observed number of correct new absences was also greater than the predicted number. Using a binomial test, we determined that both of these divisions were statistically significant. Therefore, a significant number of what appeared to be errors of classification based on one year's distributional data were actually valid predictions of future distributions of the species.

Adding data from a second year resulted in a trade of one problem for another. In addition to some new occurrences being in areas previously identified as suitable, other new occurrences of each species were in transects previously classified correctly as unsuitable for that species. Absences in the second year were also noted in areas which previously had been classified correctly as suitable with data from only one year. Although these new errors were usually less frequent than expected by chance, they still outnumbered the "corrections" for both kinds of changes in the status of bird species between the two years (table 2). Clearly, the major problem affecting our ability to define quantitatively and precisely the range of acceptable habitats for each species was the high rate of species turnover from year to year on the same transects.

Table 2. Rates of species turnover per transect, and changes which were "corrections" or new errors of status relative to discriminant analysis classification.

Overall mean probability of status change from:

Year 1	to	Year 2	
Absent		Present	0.183
Present		Absent	0.164

Number of observed cases > number of predicted cases from independence of species turnover rates and errors of classification:

Correct new presences:	18 of 21 species Binomial "P" = 0.0012
Correct new absences:	16 of 21 species Binomial "P" = 0.018

Number of new correct presences = 87

Number of new errors of presence = 108

Number of correct new absences = 49

Number of new errors of absence = 87

Table 3. The mean percent of transects which were correctly classified as supporting or not supporting each species by season:

Season	Group Present	 Absent	Total
Summer	89.7	84.6	86.5
Late Summer	94.8	89.1	91.3
Fall	91.1	87.1	88.5
Winter	87.7	86.7	87.1
Spring	89.3	91.2	90.0
Total	90.8	88.0	89.0

Two-year Discriminations

In light of the high rate of species turnover on the transects, for each species each season we regrouped the transects on a new criterion; consistency of species occurrence. Three groups were formed: 1) transects where species X was recorded both years, 2) transects where species X was absent both years, and 3) transects where species X was present in one of the years but absent in the other. Discriminant function analyses were then conducted between groups 1 and 2 for each species each season.

Results of these analyses showed a marked improvement in ability to predict correctly areas which would or would not be used by each species. Regardless of season, the mean percent of transects classified correctly was always high, and the important groups of transects used consistently were even more frequently identified correctly (table 3). This high rate of correct transect classification also eliminates the two other possible sources of error in the one-year discriminations. When investigated at an appropriate temporal scale, the bird species

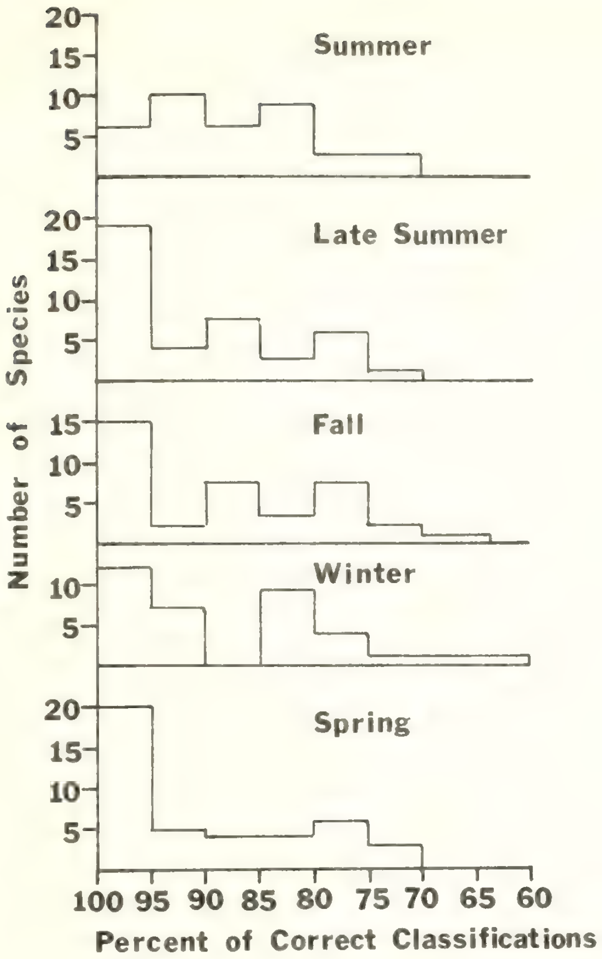

Figure 4. The number of species each season for which the classification procedures were able to correctly identify transects as used or not used with various accuracy rates. Distributional data were from two years.

generally did show habitat selectivity, and our habitat measures were adequate to detect this selectivity. The spread of the percent of species distribution predicted correctly by season (fig. 4) supports the impressions from table 3 and additionally underscores several points of general ecological significance.

One point apparent from figure 4 was the difference in the distribution of transect identifications by species between the summer and other seasons. The summer season had both the lowest mean transect identifiability and a distribution markedly more unimodal than the distribution of the transect identifications by species for the other seasons. This is, in itself, a noteworthy insight into the system we are studying.

The growing bimodality of the distribution (fig. 4) through late summer, fall, and winter is important for selecting a scale in which to undertake habitat management investigations. In summer nearly all species showed a fairly high degree of habitat selectivity, but almost none occupied areas perfectly or nearly perfectly discriminable from unoccupied areas. At other seasons the number of species with perfectly discriminable habitat-use patterns made up a substantial fraction of the community, whereas the habitat discriminability for other avian species in the community is markedly lower. The structure of the community changed from one of essentially all moderate habitat specialists in summer to a mixture of some extreme habitat specialists and other species showing quite weak habitat specificity through the fall, winter, and spring.

Considerable variability was still observed in the degree of habitat selectivity reflected by individual species. For resident species there was more variability between seasons in the discriminability of habitats used by each species (as reflected in the mean range of percent correct classifications) than between the rest of the community and a randomly selected species each season (table 4). Furthermore, the criteria of habitat selection shown by resident species, as reflected by variables with high loadings on the discriminant functions each season, changed as much as did the degree of habitat selectivity. Only 4 of 20 year-round residents had any one variable significantly different between used and unused areas for all five seasons (table 5). Information of this type is obviously of great value to persons involved in applied ecological work, and there are even a few substantial theoretical implications of these findings.

Remaining Errors

What of the errors of classification which remain: that 10% of the classifications which are still in error; and what of the distribution of the irregular transects on the discriminant axes of each bird species? Space does not allow an in-depth examination of both of these points, but we can consider the biologically most important one: areas used consistently by a species but nonetheless classified unsuitable for occupancy. In a management context, making such errors would involve the loss of habitat of high quality to the species of concern.

We again fitted the observed number of transects with no unpredicted species present, with one unpredicted species present, with two, three, and so on to the expected Poisson distribution for each season (fig. 5). In every season except winter the observed distribution deviated significantly from the predicted one, and in winter the fit was marginal. The preponderance of transects with no errors implied that the habitat suitability predictors, that is, the discriminant functions, were very accurate most of the time. Even more noteworthy, when we looked at those transects with three or four unpredicted

Table 4. Measures of the amount of variability of transects correctly classified for resident species.

Within species: Mean maximum range among seasons	Between species: Mean range around a randomly selected species each season				
	Summer	Late Summer	Fall	Winter	Spring
$\bar{X}$ = 18.16%	11.58%	13.75%	8.89%	8.57%	8.81%
s.d.= 7.25	7.22	5.62	4.30	6.39	3.89

Table 5. Criteria of habitat selection as reflected by variables significant in stepwise discriminant analyses of present vs. absent transects for resident species all seasons.

Species	Summer	Late Summer	Fall	Winter	Spring
Verdin (*Auriparus flaviceps*)	None	None	None	None	None
Cactus wren (*Campylorhynchus brunneicapillus*)	HM+,SC,HMt[1]	FHD,SC	SM+,SC	HMt	SC
House finch (*Carpodacus mexicanus*)	W,HM+HMt	C,HMt,FHD, SC	None	C,SM+,SC	None
Gila woodpecker (*Melanerpes uropygialis*)	FHD,W,C	FHD,HM+,W	FHD,O,HM+, HMt	FHD,HM+, HMt, O	FHD,HM+,C, HMt,SC,W, V5,TV
Common flicker (*Colaptes auratus*)	W,FHD,C SM+	FHD,HM+,O	V5,SC	W,HM+	TV
Gambel's quail (*Lophortyx gambelii*)	SC,HM+, W, V15,C,HMt	FHD	SC,FHD	V15	V15,V5, FHD,C, SM+,SC
Ladder-backed woodpecker (*Picoides scalaris*)	FHD,V6,V15, HM+	None	None	None	V5
Roadrunner (*Geococcyx californianus*)	V5	FHD	None	None	HMt
Loggerhead shrike (*Lanius ludovicianus*)	SC,HM+,HMt, SMtV15	C,FHD	V15,V6,V5, HMt,O	FHD,W	O
Song sparrow (*Melospiza melodia*)	C,FHD,W, V15	FHD,HMt,W, C	FHD,C,SC,W, HMt,SMt,O	FHD,C,W, HMt	FHD
Mockingbird (*Mimus polyglottos*)	HM+,HMt,SC	HMt	HMt	HMt	HMt
Ash-throated flycatcher (*Myiarchus cinerascens*)	FHD,SC,HM+, O,HMt	None	HMt,FHD,V15, O,V5,V6,SM+	None	V6,TV,C
Phainopepla (*Phainopepla nitens*)	HMt,HM+,SC	HM+	HMt,SM+,V15	HMt,SM+	HMt

Abert's towhee (*Pipilo aberti*)	FHD	None	None	None	None
Black-tailed gnatcatcher (*Polioptila melanura*)	SC,HM+,C,W, HMt,V15,V6, TV	FHD,SC,W	FHD,W	FHD	TV,V6,C
Rough-winged swallow (*Stelgidopteryx ruficollis*)	W,C	None	None	None	None
Crissal thrasher (*Toxostoma dorsale*)	SC,HM+,HMt	FHD	FHD,W,V15, V5	FHD	V15,SC,C FHD,V6
Western kingbird (*Tyrannus verticalis*)	W	None	O	W	C,SM+,SMt
Mourning dove (*Zenaida macroura*)	FHD,HMt,HM+	None	None	None	V6,TV,V5, V15
White-crowned sparrow (*Zonotrichia leucophrys*)	HM+	None	HMt	FHD	V15,TV,HMt, W,HM+,SC

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[1] Variable symbols:

V6 = Foliage volume 0.1 m - 0.6 m (0.5 ft - 2 ft)
V5 = Foliage volume 1.6 m - 3.1 m (5 ft - 10 ft)
V15 = Foliage volume 4.6 m and greater (15 ft)
TV = Total foliage volume
FHD = Foliage height diversity
HMt = Total proportion of honey mesquite (*Prosopis glandulosa*)
HM+ = Total proportion of honey mesquite with mistletoe (*Phoradendron californicum*)
SMt = Total proportion of screwbean mesquite (*Prosopis pubescens*)
SM+ = Total proportion of screwbean mesquite with mistletoe
SC = Total proportion of salt cedar (*Tamarix chinensis*)
W = Total proportion of willow (*Salix gooddingii*)
C = Total proportion of cottonwood (*Populus fremontii*)
O = Total proportion of mixed other species

species present, we found that certain types of communities displayed greater than chance frequency (table 6). Specifically, honey mesquite and/or screwbean mesquite were often classed as not suitable for species which did occur; i.e., their value to wildife is underestimated, often by as many as four or more species. This knowledge can be incorporated readily into habitat management plans.

CONCLUSION: TEMPORAL SCALE

To return to one of the major questions we initially posed, the discriminant analyses from one year's occurrence data provided a frequently significant but nonetheless weak ability to predict habitat use by each species in the riparian summer community. Merely incorporating a second year's data on distribution improved the accuracy of the predictive system markedly. For ecologists interested in the habitat attributes of species or communities, we would strongly recommend that however the initial habitat suitability judgments are formed, be they from line transects, singing male perches, from spot mapping, or whatever, a single year's data are not adequate for the study. The habitat-use patterns of avian species simply show too much year-to-year variability. Furthermore, the marked changes in community organization overall, and in habitat selectivity and selection criteria of individual species between seasons, indicate that a temporal scale smaller than an entire year is also inappropriate for a complete study of wildlife-habitat relationships.

In terms of extending the use of multivariate analyses, a stated purpose of this conference, we emphasize that many of the points made here did not come from a consideration of statistical significance of the analyses, nor from a consideration of the relative contributions of various habitat measures to the discriminant functions (the two things commonly looked at first). Rather they came from a careful consideration of errors made in the classification steps and attention to the adequacy of data to truly represent the system under study. As with many other lines of scientific inquiry, it was through attention to failure of the initial approach that subsequent insights arose.

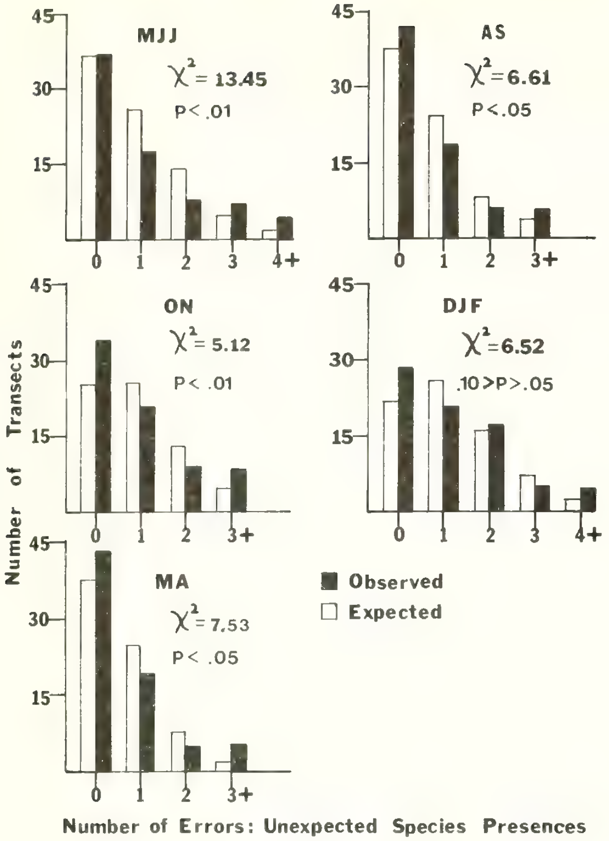

Figure 5. Fit of numbers of errors of classification of species occurrences per transect over two years to a Poisson distribution by season.

Table 6. Habitats where suitability for avian species is significantly often erroneously predicted by season.

Season	Suitability significantly often: Underestimated	Overestimated
Summer	Screwbean mesquite	None
Late summer	Honey mesquite and screwbean mesquite	Salt cedar
Fall	Honey mesquite and structure type IV	None
Winter	None	None
Spring	Honey mesquite and screwbean mesquite (P = 0.063)	None

ACKNOWLEDGMENTS

We thank J. Anderson for criticisms of the manuscript. Cindy D. Zisner typed the final draft and prepared some figures. We are grateful to the many field biologists who helped collect the data. Kurt Webb carried out the computer analyses. This work was funded through Water and Power Resources Service Grant #7-07-30-V0009.

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DISCUSSION

B.K. WILLIAMS: I want to compliment you on this focus of discriminant analysis on its classification capabilities. I would suggest that we should generally shift our perspective on this methodology more toward classification and away from group mean separation.

JAKE RICE: Thanks, and I agree with your feelings about a change in emphasis.

MARTIN RAPHAEL: Did you use equal or prior probabilities in your analysis of classification success?

JAKE RICE: Priors.

BOB CLARK: Once you have determined that a species is present, can you use DFA to classify densities (low, moderate, high) or is the system too variable? How does your food availability data tie into presence/absence on "predicted" suitable habitat?

JAKE RICE: We have had limited success with density classification; about comparable to that of the initial one-year discriminations. As you suggest, year-to-year variability in abundance is the major problem. We are including abundance predictions in the model being constructed with these DFA results, but as a step after predicting species composition for a locality. We are using a regression approach to abundance predictions, and not surprisingly, the confidence intervals are large, because of the great year-to-year variability in abundance at the same sites.

As for food availability, we have the necessary data but the analyses are not yet far enough to provide useful answers to the problem of bird distributions. Not surprisingly, insect and seed abundances are at least as variable, seasonally and yearly, as are bird distributions. Insects and seeds are also spatially highly variable, and the variation is asynchronous between sites. Tying together two such variable systems is going to be a long, slow process.

MARK BOYCE: Since your characterization of habitat is based solely on vegetation characteristics, I am concerned that other components, especially insect abundance, may vary temporally, thus possibly invalidating your remarks regarding generalists vs. specialists.

JAKE RICE: My comments on generalists and specialists were meant to apply solely in terms of habitat selection attributes. Empirically the figure shows that in late summer, fall and winter some species in the community have their used habitats clearly differentiated from areas not used, whereas other species show little habitat differentiation. It was the species showing little differentiation that I was calling generalists. Much current ecological theory would predict that these habitat generalists would be specialists on some other criterion. EVERY species could be (and probably is) a specialist on some ecological attribute, but such an approach to ecology (i.e., studying every species until one found SOMETHING on which it specialized) would provide only a limited insight into community organization, overlooking as it would all ecological attributes where a species was more generalized as being uninteresting or "invalidated" by the finding that it was a specialist on something.

JAMES DUNN: Will you clarify your statement that stepwise variable selection often resulted in entirely different variables from one season to another. Is this mainly because your habitat variables are sensitive to seasonal and/or yearly change? Or does habitat preference actually change seasonally?

JAKE RICE: To a small extent, values of the habitat measures do change seasonally. That is the case only for foliage volume measures, of course, and not tree species composition measures. The changes in significant variables reflect, in very large part, changing distributions of the species by transect, and inferentially, changing criteria of habitat selection.

JAMES DUNN: Your attack on the problem suggests that you believe that site suitability for a species is not a simple yes/no question, but rather has a range of probabilities. If so, then why not use a classification method which works by assigning a probability for each site, e.g., the multivariate model as proposed by S.H. Walker and D.B. Duncan (1967. Estimation of the probability of an event as a function of several independent variables. Biometrika 54:167-179).

JAKE RICE: We have been moving in precisely that direction with our model; predicting which species will be found in a specified area with certainty, with high probability, often, etc. The classes are pretty rough, but adequate for our users. Thank you for the reference.

PAUL GEISSLER: You have suggested sampling the same transect in several years. Resampling transects provided very valuable information for your study. However, for the different objective of determining bird habitat relationships, I think it would be advantageous to take a new sample of routes each year to provide protection against the effect of some unmeasured and possibly unmeasurable habitat effect being confounded with the effects of measured habitat variables. To put it another way, the measurements on the same route have correlated residuals.

JAKE RICE: I do not really see how "determining bird habitat relationships" is a "different objective" from what we are attempting. The major point here is that, from our data (and we think our findings are pretty general; surprisingly few data are available on the consistency of species occurrences and densities over several years at same sites) a single year's censuses are not reliable indicators of bird distributions, and therefore also are not reliable indicators of a species "habitat preferences" (or "optimal situations," if you prefer). You need multiple year's data to even get a good idea of a species' distribution pattern. Statistical considerations like correlated residuals are important, but come secondary to getting a reliable measure of the phenomenon one is trying to explain. Our point is that one year's data will not provide a reliable measure to predict, to discriminate or otherwise to statistically manipulate.

E. JAMES HARNER: Just a comment. The probabilities of misclassification tend to be underestimated in discriminant analysis. Bias can be estimated by a leave-one-out strategy or the bootstrap method (Efron, B. 1979. Bootstrap methods: another look at the jackknife. Annuls of Statistics 7(1):1-26).

A SYNTHETIC APPROACH TO PRINCIPAL COMPONENT ANALYSIS OF BIRD/HABITAT RELATIONSHIPS[1]

John T. Rotenberry[2] and John A. Wiens[3]

Abstract.--The application of principal components analysis (PCA) to bird/habitat relationships has essentially followed two paths: 1) species are ordinated based on PCA of average habitat values for individuals; 2) plots ordinated based on their average habitat values, and species' abundances on those plots correlated with the resulting component axes (which presumably reflect underlying environmental gradients).

Our proposed synthetic method is plot-based, but requires that sample points within plots be classified as lying within or outside of each individual species' area of use. As in (2), the total environmental variation, or multidemensional "habitat space", is defined by PCA of plot habitat values. However, rather than subjecting habitat values for each species to an independent PCA as in (1), a simple methodology may be used to map each species in the habitat space described by the plot PCA.

Several advantages accrue to mapping species and plots in the same environmental space. By graphing contours of species densities in this multidimensional space, patterns of abundance/habitat relationships that are not apparent from simple correlational analysis may emerge. Comparisons of plot means with values for individual species within a plot may reveal active habitat selection, or even consistent patterns of within-plot habitat partitioning between two species. Comparisons of density contours may suggest the presence of biological interactions, such as competition or ecological replacement, between two or more species.

The use of this technique is illustrated by analysis of 22 structural habitat variables collected at 26 North American grassland and shrubsteppe sites.

Key words: Birds; density contours; gradient analysis; principal components analysis; shrubsteppe; vegetation structure.

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INTRODUCTION

The use of principal components analysis (PCA) in describing patterns of avian habitat occupancy has been most fruitful, both for consideration of the adaptations of individual species (e.g., James 1971) and analysis of community composition (Rotenberry and Wiens 1980). Indeed, PCA is now routinely performed as a matter of course on a wide variety of habitat parameters, not only for birds, but also for organisms spanning a large taxonomic range [e.g., Miracle 1974 (plankton), Johnson 1977a, b (bog plants)].

The application of PCA to bird/habitat relationships has essentially followed two paths that differ, to a certain degree, in their conceptual orientations. We propose a different, somewhat synthetic approach to PCA of avian habitats that combines the virtues of both previous approaches, yet retains a relatively simple and straightforward methodology. Results from the methodology are compatible with the concept of gradient analysis (Whittaker 1967, Terborgh 1971), and can be further interpreted in such a context.

RATIONALE AND METHODS

Previous Approaches

Bird Mean Habitat Vector

The first approach to bird habitat analysis can be called the bird mean habitat vector method (James 1971, Anderson and Shugart 1974, Whitmore 1975). In this method a sampling point is usually determined by the presence of a singing male bird. Once a point is located, a variety of habitat variables, generally assumed to be of ecological relevance, are measured in the immediate vicinity. Samples are taken for a number of different species at a number of different points, the average value of each variable is calculated for each species, and this set of averages then determines the mean habitat vector. These vectors are combined into $\underline{Y}$, the matrix of standardized variables for all species, and this matrix is analyzed using standard principal component techniques (e.g., Barr et al. 1976). Resulting orthogonal components are interpreted in light of their factor loadings (the correlation between new components and original variables). Habitat relationships among species are then reconstructed by plotting the location of each species in the newly defined component space, using their factor scores as coordinates. These scores for bird species are given by

$$\underline{F}_b = \underline{S}_b' \, \underline{R}_b^{-1} \, \underline{Y}_b', \qquad (1)$$

where $\underline{R}$ is the correlation matrix of the original variables, and $\underline{S}$ is the factor structure matrix containing factor loadings (notation based on that of Thorndike 1978). The subscript b denotes bird species data.

While such a technique clearly has considerable heuristic value (as, for example, in describing relative positions of species in multivariate habitat space), it also has two potential shortcomings: 1) by focusing mainly on the simple presence of a species, the advantages of a community approach are sacrificed, and observations concerning species diversity, resource partitioning, or relative widths of ecological habitat niches are not possible; and 2) because data are collected only on the basis of a species' presence, there is no informataion concerning variation in the species' numerical abundance as habitat changes.

Site Mean Habitat Vector

The usual alternative approach is in fact community oriented, although not without drawbacks of its own (e.g., Cody 1975, Rotenberry and Wiens 1980). The method begins with selection of a large series of plots or transects, generally chosen to be representative of variation in either some set of habitat variables or some set of bird species. Habitat variables of interest are measured at a number of randomly selected points on each plot and their average taken to yield what may now be called the mean habitat vector for the site. All plots are combined in $\underline{Z}$, the set of standardized variables for plots, and PCA is performed. The factor structure matrix again provides interpretation of the components and sites are ordered in this multidimensional space by their factor scores, given by

$$\underline{F}_s = \underline{S}_s' \, \underline{R}_s^{-1} \, \underline{Z}_s' \qquad (2)$$

where $\underline{S}$ and $\underline{R}$ are the factor structure matrix and correlation matrix for site habitat data (denoted by the s subscript).

Because these are plot-based samples, each site also has associated with it species abundances, diversities, or any other attribute of the avian community one cares to calculate, and these can then be correlated with site factor scores. Significant individual correlations are generally interpreted as representing species' responses to the multidimensional habitat spectrum represented by the site ordination. If species diversity seems to vary in some meaningful manner after the sites have been ordered, then one can speculate about the nature of community organization along the gradient. These sorts of interpretations are not possible under the bird mean habitat vector method, but unfortunately their gain is offset by loss of some information about individual species. Because a species cannot be considered separately from a site, the point for that site represents all species simultaneously. If there is any within-plot habitat selection or partitioning by species, for example, this will be completely obscured, and any generalizations that one might want to make about species' relationships could be compromised.

Synthetic Approach

The technique we propose combines what we think are useful elements of both site and species ordinations. Although the methodology is largely based on site-oriented sampling, slight modifications of traditional methodology yields data that are compatible with the species-oriented approach as well.

As in the site-oriented approach, a series of sites are selected that encompass some environmental range in which one is interested, and attributes of both habitat and bird populations on these sites are measured. In the course of estimating bird densities, it is generally possible to estimate microhabitat or within-plot use by the individuals of a species as well. If, for example, individuals are territorial, this becomes a simple exercise in mapping territorial boundaries. Superimposed upon this are locations of the random points at which habitat variables are measured. These points may be characterized as lying within or outside of the area used by a species (e.g., Wiens 1969), and those that lie within the use-area can be used to create a mean habitat vector for that species at that site. These vectors will likely differ for different species at the same site (depending on the degree of within-plot spatial or habitat overlap between them), or for the same species at different sites. To the extent that a species is nonrandomly selecting habitat within the plot, its vector will differ from that of the plot as a whole. The plot or site mean vector, of course, is determined by all points.

The multidimensional environmental space in which all samples have been taken is defined by a PCA of the matrix of standardized variables for the sites, $\underline{Z}$, and as such does not differ from that presented above (equation 2). PCA is still picking out the major patterns of covariation in habitat variables that are latent within our overall selection of plots. One elects, of course, to concentrate on those components that are relatively strong (as evidenced by the relative magnitude of their eigenvalues) and meaningful, in that the patterns of their factor loadings appear to make some sort of ecological sense. Because habitat variables are in fact environmental measures, the components can be interpreted as representing real-world ecological gradients, and one can begin to apply concepts of gradient analysis to the sites, and now to the species as well.

The next step is to plot species along the same gradients. To do this, new factor scores are calculated using the factor structure matrix and correlation matrix from the habitat variables at sites, and the matrix of standardized variables from birds. Thus,

$$\underline{F}_b = \underline{S}_s' \, \underline{R}_s^{-1} \, \underline{Y}_b', \qquad (3)$$

where all matrices are as in equations (1) and (2). Resulting factor scores thus map the habitat selection of birds ($\underline{Y}_b$) onto the multidimensional environmental gradients defined by sites ($\underline{S}_s$ and $\underline{R}_s$). In other words, sites are used regardless of their species composition to determine the habitat patterns, then the distribution of the birds is plotted along these patterns, regardless of the sites on which they occur.

There are several advantages to this methodology. First is that as data are collectd from relatively large plots or transects, the community-oriented attributes that are lacking in the species-specific approach are retained, as well as estimates of individual species abundances. At the same time, however, single species may be ordinated or otherwise related to one another on the basis of species-specific, not site-specific, responses to the multivariate habitat gradient. The second major advantage is that although species at a site are analyzed in the same environmental space as the site, they need not be equated with that site's mean values. This means, for example, that within-plot habitat selection will not be obscured (fig. 1). Under normal site-based analysis, the point that represents the plot also represents, in this case, three species. By this synthetic method, however, if a species occupies a distinctly different subset of habitat than the average for a site on which it occurs, such will be readily apparent by the degree of departure of the species' position from the site's position in the PCA-space (fig. 1). Because the point for the site represents all species, any sort of within-plot habitat partitioning between them that may be occurring will be obscured using the site mean habitat vector approach. Such partitioning may be detected under the synthetic methodology, however, if there are consistent patterns of displacement of two species that otherwise co-occur at a number of sites (e.g., species 1 and species 2 in fig. 1).

Perhaps one of the most interesting properties of site-oriented analyses arises from the fact that each site-specific point for a species can be associated with that species' density at the site as well. By plotting these densities on the derived component axes, one can begin to build a picture of the quantitative distribution of species with respect to environmental gradients represented by these axes. If there are a sufficient number of sample points, contours of a species' abundance patterns may be plotted as well. The contours shown in figure 2 present a considerably stylized example, but they can be used to demonstrate some patterns that might arise from an analysis of this sort. This set of contours, for example, shows this species' numerical response to the derived habitat gradients, a response that is unlikely to be detected through any correlational analysis because of its intrinsic nonlinearity. Further, projection of contours onto each of the axes separately indicates that this species is rather

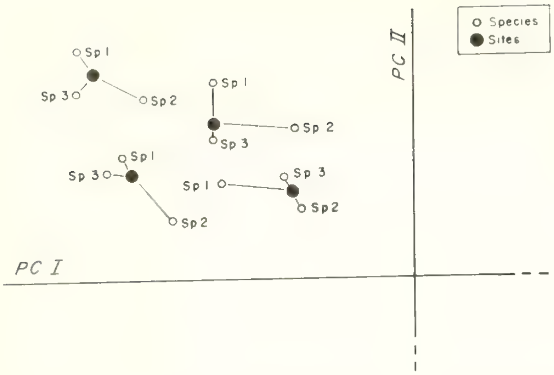

Figure 1. Hypothetical species and sites plotted in environmental space defined by the first two principal components (PCI and PCII) of site-based environmental variables. Lines connect species to sites on which they occurred.

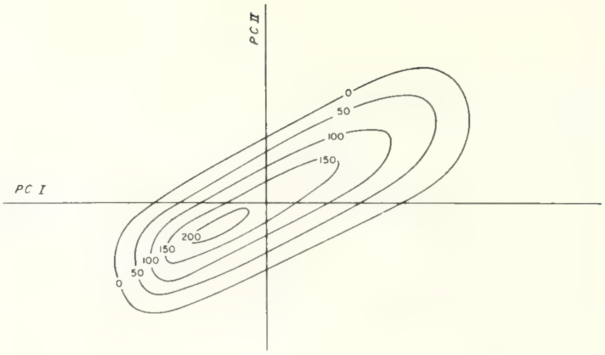

Figure 2. Hypothetical contours of species abundance patterns plotted in environmental space defined by the first two principal components (PCI and PCII) of site-based environmental measures. Contours represent isopleths of density (individuals/km²).

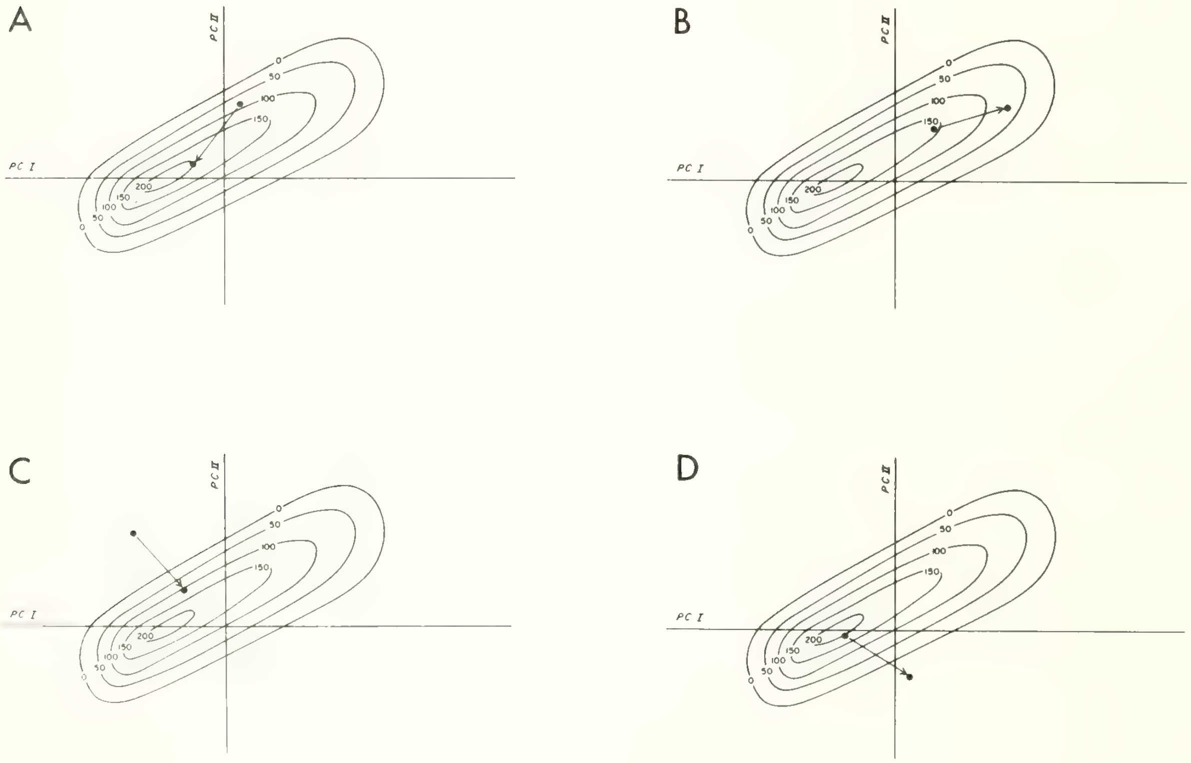

Figure 3. Hypothetical contours of species abundance patterns. Axes and isopleths as in figure 2. Arrows denote change in site characteristics as a result of habitat alteration. Changes in site characteristics may effect the following changes in a species' abundance at the site: A-increase; B-decrease; C-local invasion; D-local extinction.

generalized with respect to its distribution along these gradients. Although still maintaining the same basic configuration of contours, a different species, on the other hand, might occupy a relatively wide range on one axis but a much narrower range on the other--we can thus identify what may be called axes of specialization and generalization.

Perhaps the most interesting aspect of these contours is their potential in habitat management predictions. Insofar as one has some idea of how an environmental alteration will affect a site's location along each of the gradients--that is to say, to the degree that one can predict how a site will "move" in multidimensional habitat space after some sort of treatment--then one should be able to estimate the effect of that treatment on a species' population. For example, any sort of alteration that caused a plot to move in habitat space as indicated in figure 3A would likely result in an increase in abundance of this hypothetical species, while a different change (fig. 3B) may be much more likely to result in a decrease. We might even be able to predict changes in habiat that would lead to invasion of a species into the area (fig. 3C), assuming, of course, that it were biogeographically feasible for it to do so. Perhaps most important from a management standpoint, one might be able to define a habitat alteration that would lead to a species' local extinction (fig. 3D).

The sorts of contours depicted in figure 3 are, of course, stylized, and more often than not those derived from sets of real data are likely to deviate markedly from such smooth patterns. Certainly one of the biggest contributors to an uneven species distribution will be uneven sampling intensity with respect to the derived gradients; unfortunately such omissions are apparent only after the fact and are thus difficult to control. Other reasons, however, are more biological in nature. For example, one may sample at the periphery of habitat that is suitable for a species and thus may map only a portion of its contours (fig. 4A). Alternatively, a species may be distributed in a non-Gaussian fashion along both habitat gradients (cf. Colwell and Futuyma 1971), which would yield a pattern similar to that of figure 4B. The most extreme expression of this type of response would be a species' recognition of an environmental discontinuity or ecotone on what are otherwise statistically continuous gradients. Such an ecotonal response would likely be evidenced by a very rapid change in a species' abundance over an apparently short environmental distance (fig. 4C). On the other hand, such a pattern might also correspond with sharp abutment of one species upon another (fig. 4D). Although such a pattern may still reflect an ecotonal response, some sort of biological interaction between the two species, such as competition, becomes more likely. This pattern also identifies habitat in which investigations of such interactions should be conducted. Experiments or other comparative analyses conducted in such areas identified by this technique are likely to be more rewarding than those conducted in locales randomly chosen throughout the species' ranges.

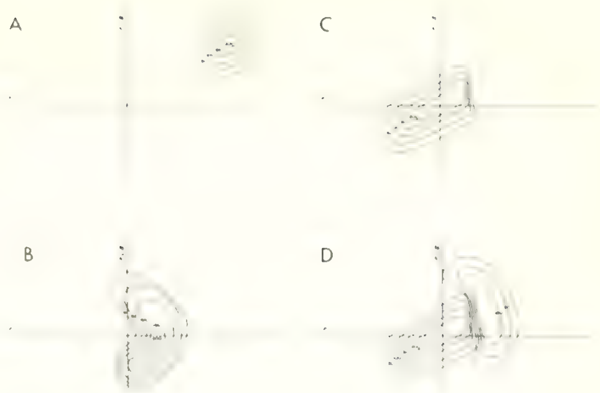

Figure 4. Hypothetical deviation from the "normal" species contours of figures 2 and 3. Axes and isopleths as in figure 2. A-Species peripheral to habitat samples. B-Non-Gaussian distribution along both environmental gradients. C-Species perceives and responds to "ecotone" on otherwise statistically continuous gradient. D-Competitive interaction between species results in habitat displacement.

If one is inclined to treat the derived gradients as representing habitat niche axes of one sort or another [and there seems to be ample reason to do this for birds (Rotenberry, 1981)], then there arises yet another set of calculations that can be made. Niche width, for example, can be estimated from some measure of dispersion around the species' centroid in multivariate space. Niche overlap between species may also be calculated, incorporating both distances between two centroids and changes in the species' contours as well. While we offer no speculation on the specific form such breadth and overlap statistics might take, the distributions of species in this environmental space will likely, we think, provide a fertile field for the application of many traditional (and even nontraditional) niche metric manipulations.

AN EXAMPLE: NORTH AMERICAN STEPPE AVIFAUNA

We would now like to provide a brief demonstration of the application of this methodology and some of its concepts to a real set of data, although unfortunately not one originally collected explicitly for this purpose. The data come from a collection of 26 grassland and shrubsteppe sites scattered throughout middle and western North America, representing a wide array of steppe vegetation types (fig. 5). Sampling methodology, site locations, species lists and abundances, descriptions of variables, etc. are fully detailed elsewhere (Rotenberry and Wiens 1980). At each plot we set up a 10-ha grid, mapped the territories of all breeding birds, and measured habitat variables. In this particular

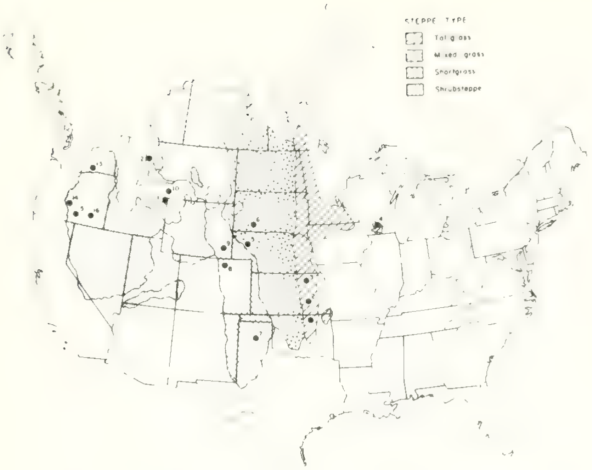

Figure 5. Location of avian censuses used in this analysis. Numerals keyed to table 1 in Rotenberry and Wiens (1980). Steppe types generalized from Küchler (1964).

study we were interested in the role of spatial heterogeneity, or patchiness in vegetaion structure, in determining distribution and abundance of grassland birds and the structure of their communities. The 22 variables that were measured fell into two basic categories: coverage variables (simply the percent coverage of various physiognomic classes, such as shrubs, grasses, forbs, or bare ground) and structural variables. Structural variables are also physiognomic in nature, but have the additional property of "dimension"; that is to say, variation in a structural measure is generally associated with variation in either a horizontal or a vertical plane. Ultimately 10 horizontal heterogeneity indices, 5 vertical indices, and 7 coverage classes were considered. The results, given here in the most basic form (table 1), were somewhat surprising in that a very distinct separation between the vertical and horizontal indices were observed; 9 of 10 horizontal indices loaded high on the first axis (41% of total variation), while all 5 vertical indices loaded high on the second (22% variation). Increasing horizontal heterogeneity was associated with increasing coverage of shrubs and bare ground, and decreasing coverage of grass and litter. Vertical heterogeneity varied slightly with changing forb coverage. Together, these two axes accounted for almost two-thirds of the total variation. We thus interpreted these components as representing two largely independent gradients in vegetation structural heterogeneity--a major axis of horizontal patchiness and a minor axis in vertical patchiness.

The sites tended to sort themselves into broad classes along these axes in horizontal and vertical heterogeneity (fig. 6A). Tallgrass sites evidenced substantial vertical heterogeneity, but relatively little patchiness in a horizontal plane. Shrubsteppe sites generally showed as much

Table 1. Factor loadings of vegetation principal components. Only those loadings greater than 0.40 (analogous to a correlation significant at the 0.05 probability level) are shown; only the first two of five factors with eigenvalues greater than 1 are shown. Complete details of the analysis, including explanations of variables, are given by Rotenberry and Wiens (1980).

	Factor:	I	II
	Eigenvalue:	9.02	4.94
Vegetation variable	% σ:	41.0	22.4
	Σ % σ:	41.0	63.4
Structural-horizontal			
HIT-10		0.46	0.44
LITDEP		-0.71	0.52
CVTOTHIT		0.83	
CVMAXHGT		0.84	
CVLITDEP		0.80	
CVTOTHGT		0.50	
CVHGTDIF		0.68	
HITS-HI		0.93	
LIT-HI		0.69	
DIST-HI			0.73
Structural-vertical			
TOTHITS		0.56	0.56
MAXHGT			0.77
EFFHGT			0.86
TOTHGT			0.88
HGT-HI			0.70
Coverage			
Grass		-0.87	
Forb			0.40
Shrub		0.80	
Bare		0.92	
Litter		-0.82	

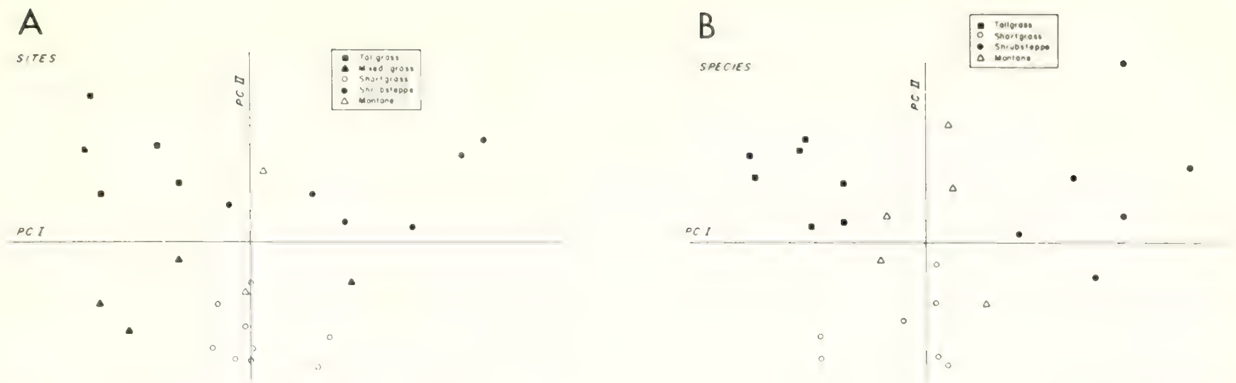

Figure 6. Distribution of steppe bird census sites (A) and bird species means (B) in environmental space defined by the first two principal components (PCI and PCII) of 22 site-based habitat structure variables. PCI represents increasing horizontal heterogeneity; PCII represents increasing vertical heterogeneity.

vertical heterogeneity as the tallgrass ones, but differed markedly in being much patchier horizontally. Shortgrass sites were intermediate in horizontal heterogeneity but, as one might expect, showed very little vertical variability. Mixed-grass sites were the most varied in their structure, with some positioned intermediate to shortgrass and tallgrass plots, while another more closely resembled shrubsteppe sites in structure. Montane sites were intermediate as well.

Figure 6B shows bird species plotted in the same space; each point represents the average of a species' factor scores for all of its occurrences combined without regard to its abundance. Not surprisingly, species that are identifiable as being largely tallgrass, shortgrass, or shrubsteppe species are generally found in the same areas of PCA-space as their sites. Of more interest, of course, are some details that go into generating these means. For example, figure 7 reprsents both sites and birds for four tallgrass and four shrubsteppe samples. (Scientific names of all species are given in appendix I.) It is apparent that a number of shrubsteppe species are not very close to their site means, and indeed some sites appear to have a great deal of dispersion around them. Although tallgrass species did not appear as dispersed, dickcissels and grasshopper sparrows did demonstrate a consistent pattern of within-plot partitioning, with the latter found in vegetation of less vertical heterogeneity but greater horizontal patchiness. The co-occurring eastern meadowlark, however, seemed to be positioned independently.

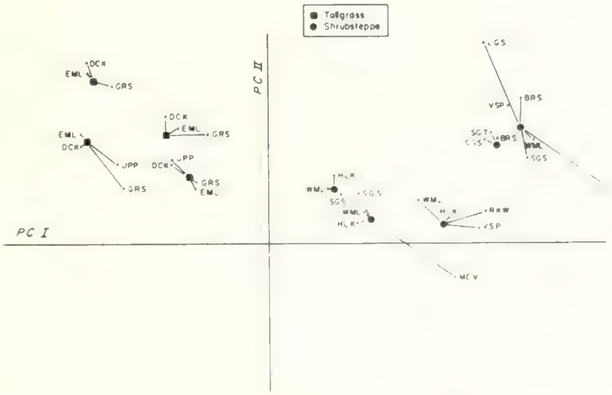

Figure 7. Distribution of tallgrass and shrubsteppe bird census sites and individual bird species from those sites. Axes as in figure 6. EML = eastern meadowlark, DCK = dickcissel, GRS = grasshopper sparrow, UPP = upland plover, WML = western meadowlark, HLK = horned lark, SGS = sage sparrow, MDV = mourning dove, RKW = rock wren, VSP = vesper sparrow, SGT = sage thrasher, BRS = Brewer's sparrow, LGS = loggerhead shrike.

Contour intervals for the species show a wide variety of patterns (figs. 8-15). Our collection of sites appears to have almost exactly centered on the habitat distribution of western meadowlarks (fig. 8), and this pattern, in retrospect, is perfectly consistent with most of what is known about the behavior, habitat selection, and

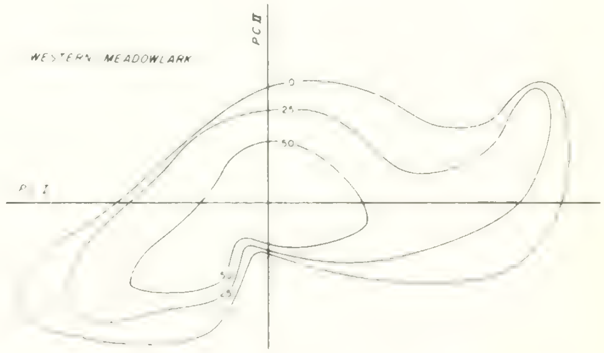

Figure 8. Distributional pattern of western meadowlarks. Axes as in figure 6. Isopleths as individuals/km².

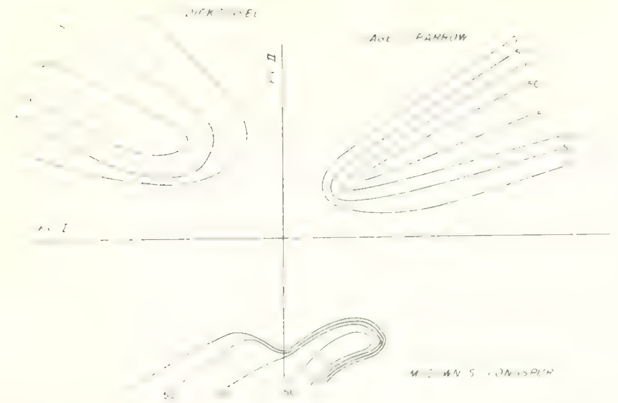

Figure 9. Distributional pattern of dickcissels, sage sparrows, and McCown's longspurs. Axes and isopleths as in figure 8.

geographical distribution of this species (Lanyon 1956, and personal observation).

It also appears that the range of habitats sample was only peripherally used by several species. For example, the dickcissel (a tallgrass prairie species), sage sparrow (a shrubsteppe bird), and McCown's longspur (abundant in shortgrass) all seem to have centers of distribution that lie at the edge or even outside of the limits of habitat gradients defined here (fig. 9). Presumably, then, if data were collected in more extreme shrubsteppe vegetation, we would be able to define the limits of sage sparrow distribution more accurately. The most extreme example of peripheral species are those that occurred on just one of the 26 plots we sampled (fig. 10). If a line is graphed that encloses all the site mean values for these gradients, it is apparent that these species all lie beyond that boundary, indicating that even at those sites on which they did occur they were occupying peripheral habitat. It likewise is assumed here that if sampling effort were increased away from this boundary, more sites at which these species occur would be encountered.

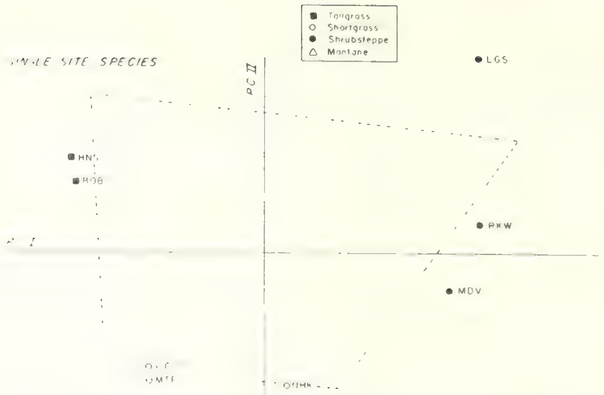

Figure 10. Distributional pattern of species that occurred at only a single census site. Species associated with montaine meadows have been omitted. Axes as in figure 6. Dashed line encloses all site mean values (figure 6A). HNS = Henslow's sparrow, BOB = bobolink, CGL = chestnut-collared longspur, MTP = mountain plover, NHK = common nighthawk, MDV = mourning dove, RKW = rock wren, LGS = loggerhead shrike.

Horned larks, present in both shrubsteppe and shortgrass habitats, apparently increase in abundance as the habitat becomes more uniform in both dimensions (fig. 11). This is consistent with our own observations of the species, which suggest that the lark's ultimate idea of habitat nirvana is the uniform monotony of a paved parking lot.

Some patterns of contours are more difficult to interpret. Brewer's sparrows, for example, evidenced a rather discontinuous distribution (fig. 12). While we have searched for another species that might fit in the gap, none of the species enounterd in our censuses througout the North American steppe vegetation showed a reciprocal distribution in this area. At this time we can only surmise that there may be some sort of biogeographical constraint to Brewer's sparrows filling in the vacancy, or that perhaps

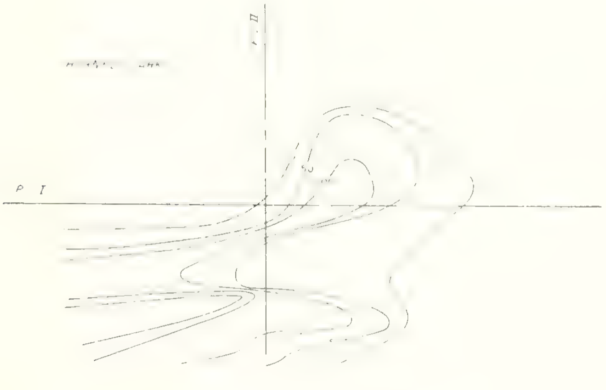

Figure 11. Distributional pattern of horned larks. Axes and isopleths as in figure 8.

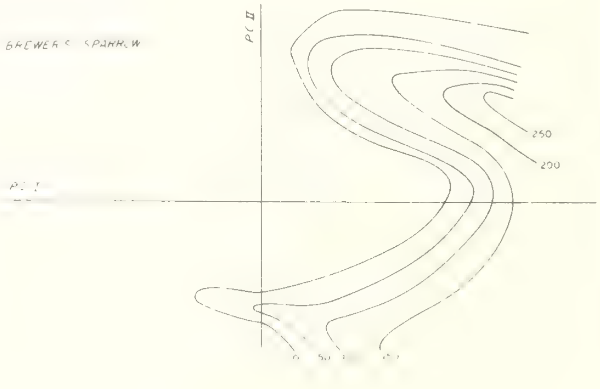

Figure 12. Distributional pattern of Brewer's sparrows. Axes and isopleths as in figure 8.

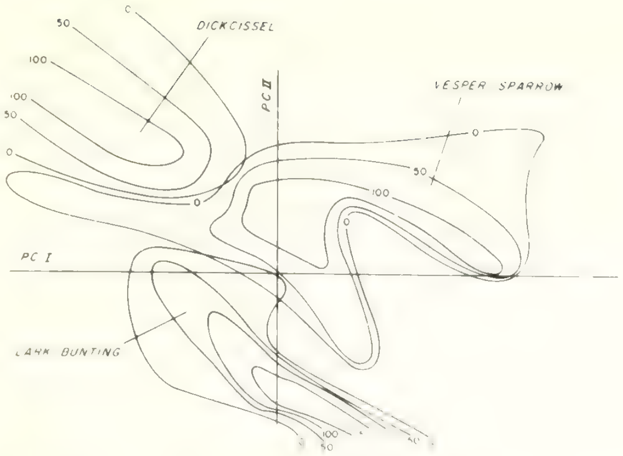

Figure 13. Distributional pattern of vesper sparrows, dickcissels, and lark buntings. Axes and isopleths as in figure 8.

populations in the two rather disjunct habitat types represent different ecological races or even incipient subspecies.

The precise habitat affinities of vesper sparrows have defied ready generalizations, and their distribution along these synthetic habitat gradients (fig. 13), when considered by itself, adds little to a more precise definition. It is interesting, however, to plot the vesper sparrow simultaneously with the dickcissel (a tallgrass species) and the lark bunting (a shortgrass species) (fig. 13). While one cannot conclude from this analysis what mechanism might ultimately be responsible for these observed distributional patterns, they certainly appear to be nonrandom.

One may also examine situations where nonrandom patterns of distribution might be predicted a priori, such as might result from competitive interactions. Eastern and western meadowlarks, for example, are congeneric and are thought to express a number of competition-induced relationships. Their contours, while largely exclusive, do show some overlap (fig. 14). Although no really clear pattern is present in terms of a sharp abutment or exclusivity, we could predict that sites that fall within the particular area where density overlap is greatest are where interspecific territoriality is likely to be most intense. Although dickcissels and grasshopper sparrows appeared to partition individual tallgrass plots (fig. 7), their pattern of contours (fig. 15) suggests little partitioning on a regional scale and instead seems indicative of independent differential habitat selection.

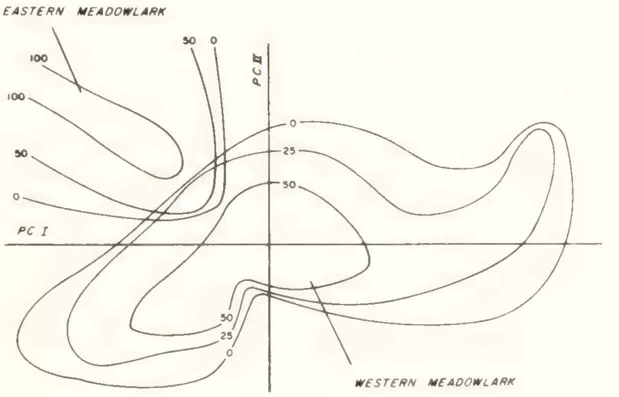

Figure 14. Distributional pattern of eastern and western meadowlarks. Axes and isopleths as in figure 8.

Finally, one can examine the predicted effect of some major alteration in some part of the steppe environment; say, for example, a decision were made to mow a tallgrass prairie? One expects a tremendous drop in vertical heterogeneity as the grasses are all cut flat, with perhaps a slight increase in horizontal patchiness as new areas of bare ground open up following removal of forbs and small shrubs. By superimposing this change upon the species' contours, changes in species abundances can be predicted (fig. 16). Clearly the tallgrass species such as dickcissels (fig. 16A) and eastern meadowlarks (fig. 16B) are likely to disappear altogether, while species abundant in habitat with low vertical heterogeneity, like horned larks (fig. 16C) or lark buntings (fig. 16D), will probably increase considerably if there are no biogeographical constraints to their response to this habitat alteration. Grasshopper sparrow densities may change (fig. 16E), but it seems unlikely that the species would disappear altogether. In the case of the western meadowlark, however, predictions could be equivocal (fig. 16F); this will depend both upon accuracy in estimating how an altered site will "move" in habitat space and upon proximity of the new site position to contours representing an area of fairly rapid change in a species' abundance.

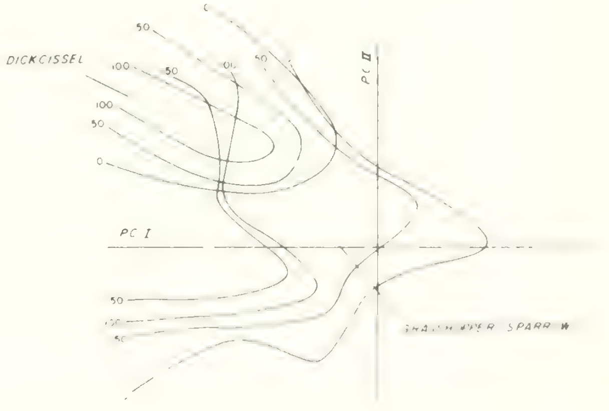

Figure 15. Distributional pattern of dickcissels and grasshopper sparrows. Axes and isopleths as in figure 8.

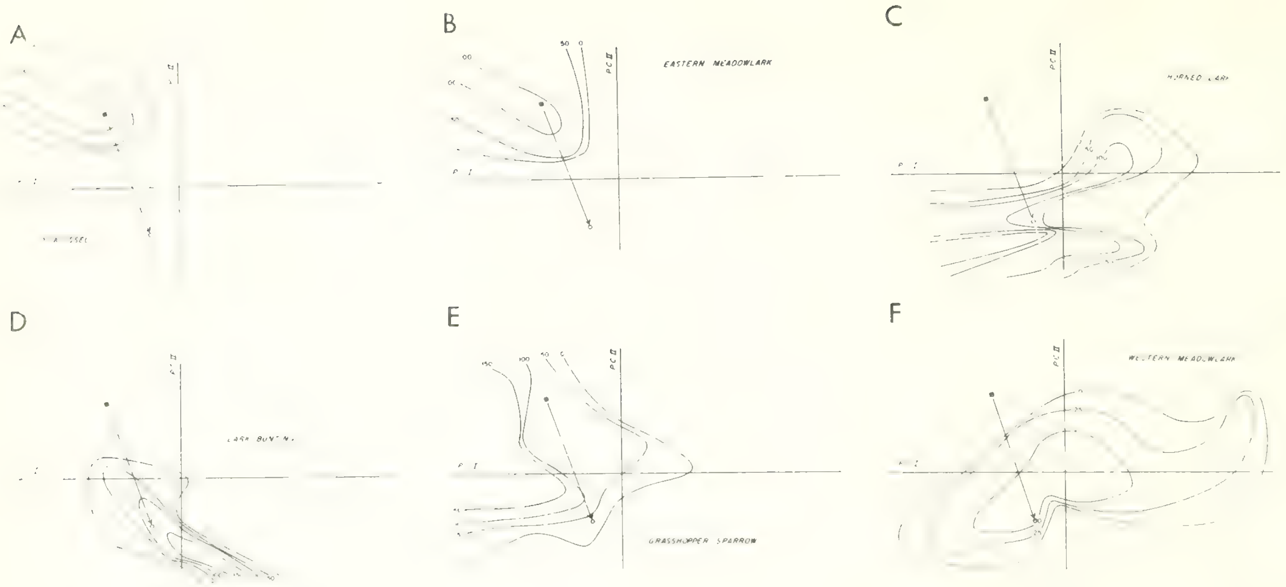

Figure 16. Responses of affected species to hypothetical structural changes and associated multidimensional movement of a tallgrass site that is subjected to mowing. A-dickcissel, B-eastern meadowlark, C-horned lark, D-lark bunting, E-grasshopper sparrow, F-western meadowlark.

CONCLUSIONS

We hope to have made it clear that, even with a set of data that was not taken with the methodology in mind, our technique of combining the individual species approach with one that is plot-oriented is feasible; indeed, there may be sets of existing bird/habitat data to which it may be applied. Analysis certainly need not be confined to physiognomic variables as we have done here, but can be extended to whatever environmental or habitat variation one thinks is important in affecting species distributions and relationships. Although certain biological objections can be raised regarding application of PCA to either species- or plot-oriented data (Johnson 1981), we believe this new technique, combined with judicious selection of variables, appropriate sample sizes, and other attention to statistical niceties, may ameliorate these objections substantially. One must bear in mind that the technique of PCA is descriptive rather than inferential and that it basicially provides us a sophisticated "multivariate natural history". We think that such descriptions will ultimately prove robust with respect to what is already known about the particular set of species described and that they will be capable of generating new insights for those that employ them.

ACKNOWLEDGMENTS

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Appendix I. Scientific names of all birds mentioned in text or figures.

Mountain plover	Eupoda montana
Upland plover	Bartramia longicauda
Mourning dove	Zenaida macroura
Common nighthawk	Chordelis minor
Horned lark	Eremophila alpestris
Rock wren	Salpinctes obsoletus
Sage thrasher	Oreoscoptes montanus
Loggerhead shrike	Lanius ludovicianus
Bobolink	Dolichonyx oryzivorus
Eastern meadowlark	Sturnella magna
Western meadowlark	Sturnella neglecta
Dickcissel	Spiza americana
Grasshopper sparrow	Ammodramus savannarum
Henslow's sparrow	Passerherbulus henslowii
Lark bunting	Calamospiza melanocorys
Vesper sparrow	Pooecetes gramineus
Sage sparrow	Amphispiza belli
Brewer's sparrow	Spizella breweri
McCown's longspur	Calcarius mccowni
Chestnut-collared longspur	Calcarius ornatus

DISCUSSION

BOB WHITMORE: How did you compute the density contours? The smooth curves that you presented would seem to indicate many ($>10^8$) data points. How many points per species did you have?

JOHN ROTENBERRY: Not nearly as many as we would have liked, especially for species whose distributions take them off the edges of the habitat space. The curves were initially drawn using strict linear interpolation between points; I subsequently smoothed them by eye for this presentation. To a considerable extent it represents artistic license tempered by the interpolated realities and biological intuition.

BOB WHITMORE: You had some species with "peripheral ranges" on your ordinations. How do you know that the observed distributions are not just an artifact of the variables being measured?

JOHN ROTENBERRY: We cannot know for sure, but it seems likely due to biogeographical considerations and the distribution of our sites.

E. JAMES HARNER: How did you scale the variables in your PCA analysis? Did you only use the correlation matrix?

JOHN ROTENBERRY: The variables were all normalized using either log or arcsin square root transformation. I only used the correlation matrix for PCA, which is analogous to using the covariance matrix of standardized data. The component axes were also rotated using varimax.

BOB WHITMORE: Given the overlap problems when using centroid distances, why not use a multivariate measure of niche overlap?

JOHN ROTENBERRY: I think that would be the best approach.

JAMES DUNN: How the species counts balance each other as a function of site properties is an interesting question. Does your analysis reflect this? Why not try the GSK model as implemented by PROC FUNCAT(SAS)? One nice feature of the model is that it would allow formal tests of the effects of habitat variation on relative frequencies of the species. In particular, the total bird count/ plot could be used as a predictor to see if site productivity affects the relative composition of the species. The only difficulty I see with the FUNCAT is zero counts which you may have. Potentially a maximum likelihood solution could handle that using "working values."

JOHN ROTENBERRY: In the paper where the data were originally described, we did test correlations of species diversity, richness, and evenness with each of the component axes. Diversity did significantly increase with incoming vertical heterogeneity, but varied independently of horizontal heterogeneity. Richness and evenness were not significantly correlated with either axes. With respect to examining relative frequencies, I think it might be worthwhile, but we are, in fact, plagued with zero counts throughout the bird data set. I'm not familiar with FUNCAT, so I don't know how the use of "working values" will affect the outcome.

CHARLES SMITH: When making measurements in the field, how does one differentiate between the extremes of the "niche-habitat continuum," that is, are habitat variables distinguished from niche variables when measurements are taken?

JOHN ROTENBERRY: I suspect that in general we are not dealing with the extremes, but that instead most of the variables we chose to measure reflected both aspects. My feeling is that the synthetic component axes do represent habitat gradients, and that (for birds at least) habitat is a niche dimension, for the reasons I suggested earlier in this workshop.

PAUL GEISSLER: Looking at your figures, I noted that many of the frequency ellipses were oriented at about 45° to the axis. Perhaps the interpretability of the axes for the birds might be improved if the axes were rotated parallel to the orientation of the ellipses.

JOHN ROTENBERRY: There are two problems with doing that. First, if we rotate the axes with respect to the birds, we destroy the relationships among the variables and change the interpretation of the axes in some unknown way. This would not be the same thing as varimax or orthomax rotation. Second, the ellipses do represent the relations of the bird species to the derived axes. If a species shows a response to both horizontal and vertical heterogeneity, we expect frequency ellipses to be oriented just this way.

ROBUST PRINCIPAL COMPONENT AND DISCRIMINANT ANALYSIS OF TWO GRASSLAND BIRD SPECIES' HABITAT[1]

E. James Harner[2] and Robert C. Whitmore[3]

Abstract.--Outliers in multivariate data can have pronounced effects on the interpretations and conclusions of statistical analyses. However, data is rarely examined for outliers, due in part to the difficulty in discovering them if the dimensionality of the variable space is greater than two or three. We also do not believe that researchers are aware of the severity of the problem that outliers create.

Techniques are currently being developed which are robust to small departures from the assumed model and, in particular, to outliers. The robust methods summarized in this paper are simple extensions of maximum likelihood estimators of the mean vector and covariance matrix assuming an underlying normal distribution. In essence, they are weighted versions of maximum likelihood techniques in which weights are determined iteratively based upon the size of Mahalanobis distances. Principal components can be determined from the robust covariance or correlation matrix. For the discriminant problem, robust estimates are determined for each group and these are substituted into Fisher's linear discriminant function.

These techniques are applied to two sparrow species on which four habitat variables were measured. These data have some outliers but the data set would not be classified as being "bad." The principal component analyses for both species resulted in less emphasis being placed on the first component for the robust techniques as compared to the classical method. Fisher's linear discriminant model depended too heavily on several outlying values. In order to improve the stability of estimates and the accuracy of future classifications, Huber's robust discriminant analysis with a cutoff value of 1.97 was adjudged to be best.

Key words: Discriminant analysis; grassland birds; maximum likelihood estimation; principal components analysis; robustness.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington, Vt.

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INTRODUCTION

Multivariate analyses often start with mean vector and covariance matrix estimates. In principal components the eigenvectors and eigenvalues are computed from the covariance matrix or from scaled versions of it. The mean vector and covariance matrix are calculated from each sample in discriminant analysis. Unfortunately, classical maximum likelihood estimators based on multivariate normal theory and least squares estimators are extremely sensitive to outlying observations.

During the past 20 years statisticians have been developing new estimators or modifying existing estimators to make them less sensitive to certain departures from the assumptions of a model. Three classes of estimators are being developed:

1) M-estimators or maximum likelihood type estimators;
2) R-estimators or rank type estimators; and
3) L-estimators or estimators based on linear combinations of order statistics.

Estimators of the above types are called robust estimators. By robustness we mean that the distribution of an estimator is insensitive against small deviations in the shape of the underlying distribution of the assumed model. This is essentially equivalent to an estimator being robust to outliers although other distributional variations are possible. In many biological sampling situations outliers frequently arise due to gross errors (bad data points) or from heavy-tailed distributions. Huber (1977a) states that "5-10% wrong values in a data set seem to be the rule rather than the exception." Since our experience with outliers in biological data is consistent with this statement, we feel robust methodologies are of great value to researchers.

A general theory of R and L-estimators is currently being developed for the univariate linear model (Hettmansperger and McKean 1977, Bickel 1973). However it is not clear how to extend these to the multivariate case. The theory of M-estimators was begun by Huber (1964). Huber (1977a, 1977b) and Maronna (1976) developed M-estimation techniques for the mean vector and covariance matrix of a single population. They derived properties of these estimators and suggested algorithms to compute them. Randles et al. (1978) studied the performance of these and other estimators in the two group linear and quadratic discriminant analysis problem. Other than these papers, little else has been done.

The intent of this paper is to apply the estimators developed by Huber and Maronna to bird habitat data. Both principal component and discriminant analyses are presented. First an introduction to M-estimators is given.

M-ESTIMATORS

Univariate Problem

For intuition the univariate location problem is considered first. Let $f(x-\mu)$ represent a density and μ the location parameter (mean) we want to estimate. $X_1, X_2, \ldots, X_n$ represents a random sample from this distribution. The maximum likelihood estimate is that value of μ which maximizes

$$L(\mu) = \prod_{i=1}^{n} f(x_i-\mu),$$

the likelihood function. It is more convenient to maximize $\ln L(\mu)$ which gives the same solution since the natural logarithm is a monotonic transformation. Thus we maximize

$$\ln L(\mu) = \sum_{i=1}^{n} \ln f(x_i-\mu) = -\sum_{i=1}^{n} \rho(x_i-\mu)$$

with respect to μ where $\rho(x-\mu) = -\ln f(x-\mu)$. Differentiating and setting the resulting expression to zero we get

$$d[\ln L(\mu)]/d\mu = -\sum_{i=1}^{n} f'(x_i-\mu)/f(x_i-\mu)$$

$$= \Sigma\phi(x_i-\mu) = 0,$$

where $\phi(x-\mu) = d[-\rho(x-\mu)]/d\mu$.

The maximum likelihood estimate, $\hat{\mu}$, solves the last equation.

The normal case is given by:

$$f(x-\mu) = (1/\sqrt{2\pi})e[-(x-\mu)^2/2],$$

$$\rho(x-\mu) = (x-\mu)^2/2-c, \text{ and}$$

$$\phi(x-\mu) = x-\mu.$$

The solution then is found by solving

$$\Sigma\phi(x_i-\mu) = \Sigma(x_i-\mu) = 0 \text{ or}$$

$$\hat{\mu} = \Sigma x_i/n,$$

the sample mean.

Maximum likelihood estimators may or may not be robust depending on the form of $f(x-\mu)$. However, the commonly used normal case is decidedly non-robust. To illustrate this, consider a sample of four from a normal distribution together with one outlier. Suppose the values are 2, 4, 10, 3.5, 3. The ρ functions of each x_i are given in figure 1 with c arbitrarily set to zero. The maximum likelihood estimate, $\hat{\mu}=4.5$, is being influenced greatly by $x_3 = 10$. On the other hand, the median, a robust estimator, has a value of 3.5. The difficulty is that we are minimizing $\Sigma\rho(x_i-\mu)$ which is quadratic in the normal case. For an outlier, x_3 say, $\rho(x_3-\mu)$ is quite large near the center of the distribution and thus the solution $\hat{\mu}$ is pulled to the right so that $\rho(x_3-\hat{\mu})$ is not so large.

Clearly this ρ function does not result in a robust estimate. How can we robustify ρ? Intuitively, it appears that at some distance symmetric about each x_i we should make ρ increase less rapidly, perhaps even level off. Various functions have been suggested by researchers and two of these are sketched in figure 2 along with the maximum likelihood ρ. Huber's function increases quadratically along with the maximum likelihood ρ until $|x-\mu| = k_1$. For $|x-\mu| > k_1$ Huber's function increases linearly. Hampel's function follows Huber's until $|x-\mu| = k_2$ at which time $\rho(x-\mu)$ begins to level off, which it does at $|x-\mu| = k_3$. The values for k_1, k_2, and k_3 can be chosen by the researcher but reasonable values are $k_1 = 1.7$, $k_2 = 3.4$, and $k_3 = 8.5$ (Hogg 1979). The analytic representations of the functions are also given in Hogg (1979).

Robustness can be characterized more easily in terms of the ϕ functions (fig. 3). To be robust the ϕ function should at least be bounded.

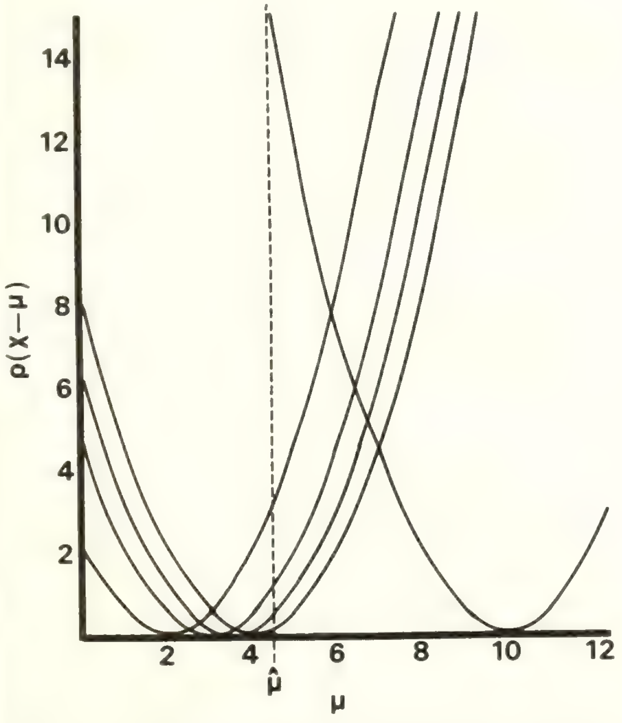

Figure 1. Normal density ρ plotted as a function of μ for each fixed x_i.

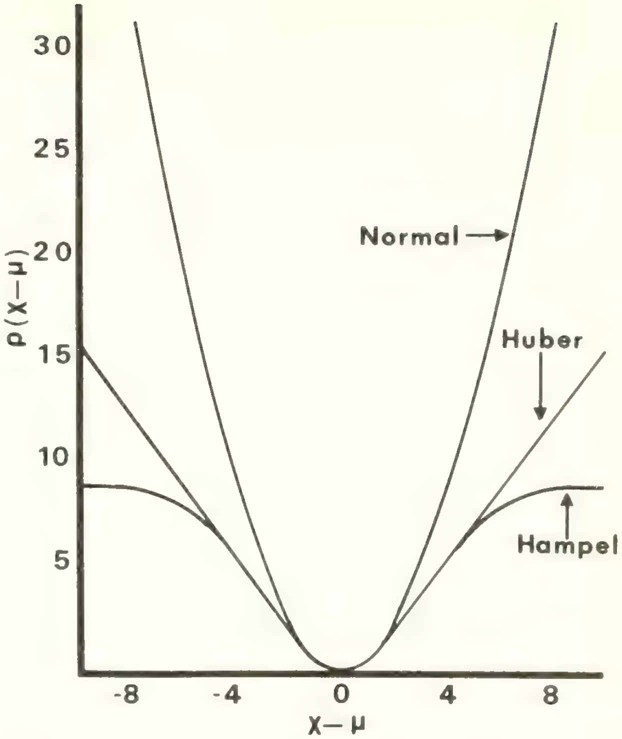

Figure 2. Normal density, Huber, and Hampel ρ's plotted as a function of $x-\mu$ with constants of $k_1 = 1.7$, $k_2 = 3.4$, and $k_3 = 8.5$.

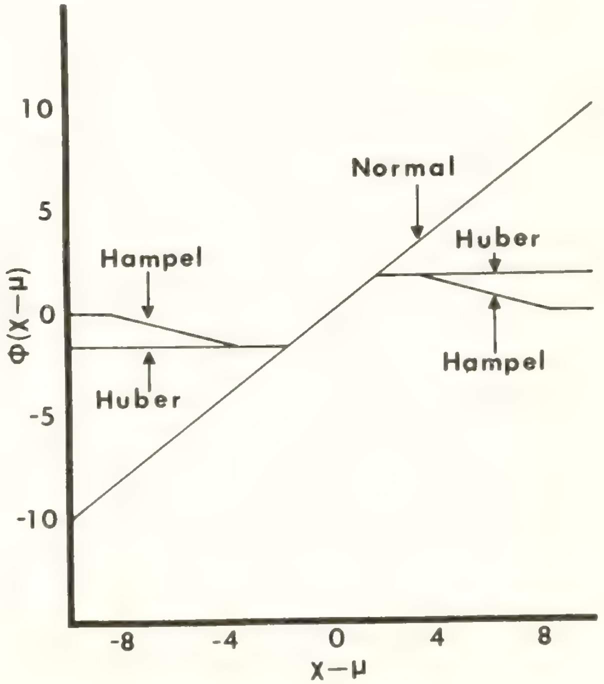

Figure 3. Normal density, Huber, and Hampel ϕ's plotted as a function of $x-\mu$ with constants of $k_1 = 1.7$, $k_2 = 3.4$, and $k_3 = 8.5$.

Note that Hampel's function even redescends to zero.

Why is the shape of the ϕ function so important? First, the influence an observation has on the estimators is proportion to ϕ for M-estimators (Hampel 1974). Thus if ϕ is unbounded as is the ϕ function in the normal case, a single "bad" value can have a great influence. Secondly, M-estimators of this type can be expressed as weighted means with the weights proportional to ϕ. That is

$$\Sigma\phi(x_i-\mu) = \Sigma w_i(x_i-\mu)$$

where $w_i = \phi(x_i-\mu)/(x_i-\mu)$.

In the normal case $w_i = 1$ for all i but the Huber and Hample estimates may have $w_i < 1$.

For simplicity we have been examining the case in which $\sigma = 1$ (i.e., the scale parameter is unity). Actually we must solve

$$\Sigma\phi[(x_i-\mu)/\sigma] = 0$$

by obtaining an ancillary estimate of σ. Generally the equation is solved iteratively starting from initial estimates, $\hat{\mu}_o$ and $\hat{\sigma}_o$. At stage j the estimate of scale is updated and the new estimate of location is then computed. The estimate of scale should be robust, such as the median absolute deviation (MAD) estimator (Mosteller and Tukey 1977).

The procedure described above can easily be extended to the regression case (e.g., Hogg 1979). Consider the model

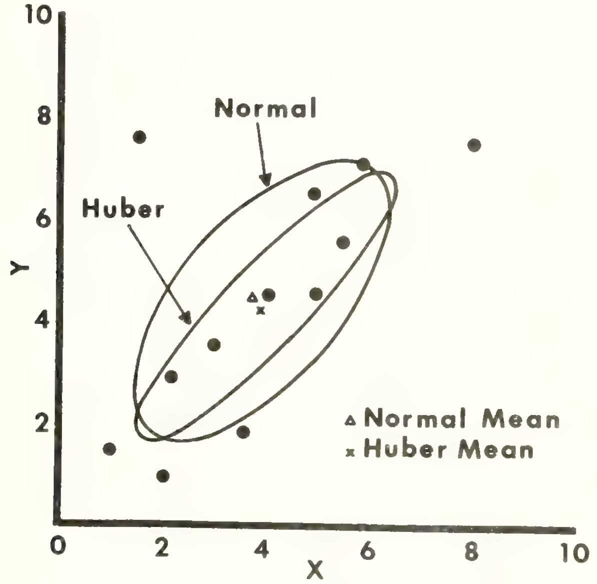

Figure 4. Example illustrating the effect of a single outlier on the mean vector and 50 percent concentration ellipse.

$$y_i = \underline{x}_i\underline{\beta}+e_i,$$

where y_i is the ith "dependent" observation, $\underline{x}_i$ is the ith 1 x p known "independent" vector, $\underline{\beta}$ is a p x 1 vector of unknown parameters, and e_i is the ith random error. We now want to solve for $\underline{\beta}$ in the p equations

$$\Sigma x_{ij}\phi[(y_i-\underline{x}_i\underline{\beta})/\sigma] = 0, \ j = 1, 2, \ldots., p,$$

where x_{ij} is the jth "independent variable" on the ith observation. Of course ancillary estimates of σ are required. The system is solved iteratively as before.

Multivariate Problem

The multivariate estimation problem is much more complicated than the univariate one. In particular, outliers in high demensional space are difficult to detect. Outliers may be apparent only on new variables which are linear combinations of the original variables. Although difficult to detect, their effect may be large. Figure 4 illustrates the effect of a single outlier on the concentration ellipse and on the sample mean vector. Notice that the sample mean vector is pulled toward the outlier. More importantly the shape of the concentration ellipse, which is determined from the sample covariance matrix, is distorted. This is important since most multivariate analyses are based on estimates of covariance matrices. The robust correlation of 0.904 more adequately expresses the relation between x and y than does the standard Pearson product-moment correlation of 0.634.

Clearly robust estimators are needed which minimize the effect of outliers. This is particularly true in the multivariate case, since variances and covariances are extremely sensitive to outliers.

Maronna (1976) and Huber (1977a, 1977b) have developed most of the theory for robustly estimating multivariate location and scale using M-estimators. Maronna characterizes M-estimators as being the solutions to the following matrix equations:

$$n^{-1}\sum_{i=1}^{n} U_1[\sqrt{d_i}](\underline{x}_i-\underline{\mu}) = 0$$

$$n^{-1}\sum_{i=1}^{n} U_2[d_i](\underline{x}_i-\underline{\mu})(\underline{x}_i-\underline{\mu})' = \underline{\Sigma}$$

where $\underline{\mu}$ is the p x 1 mean vector, $\underline{\Sigma}$ is the pxp covariance matrix, $d_i = [(\underline{x}_i-\underline{\mu})'\underline{\Sigma}^{-1}(\underline{x}_i-\underline{\mu})]^{1/2}$ is the Mahalanobis distance, and U_1 and U_2 are weight functions. In the multivariate normal case $U_1 = U_2 = 1$ for all i and the ordinary maximum likelihood estimators result, that is $\hat{\underline{\mu}} = \Sigma \underline{x}_i/n$, and $\hat{\underline{\Sigma}} = [\Sigma(\underline{x}_i-\hat{\underline{\mu}})(\underline{x}_i-\hat{\underline{\mu}})']/n$. Huber's development of M-estimators is slightly more general than Maronna's.

We used a modified form as suggested by Randles et al. (1978). Start with $\underline{\bar{x}}$ and $\underline{S}$, the ordinary estimates. Compute

$$d_i = [(\underline{x}_i-\underline{\bar{x}})'\underline{S}^{-1}(\underline{x}_i-\underline{\bar{x}})]^{1/2},\ i = 1, 2, \ldots, n.$$

Replace $\underline{\bar{x}}$ and $\underline{S}$ by weighted estimates

$$\underline{\bar{x}}^* = (\Sigma w_i \underline{x}_i)/\Sigma w_i \text{ and}$$

$$\underline{S}^* = (\Sigma w_i^2(\underline{x}_i-\underline{\bar{x}}^*)(\underline{x}_i-\underline{\bar{x}}^*)')/\Sigma w_i^2$$

where $w_i = k/d_i$ if $d_i > k$ and $w_i = 1$ if $d_i \leq k$. The procedure is iterated until the change in $\underline{\bar{x}}^*$ and $\underline{S}^*$ is sufficiently small or until a predetermined number of iterations is reached.

A graph of the weight function is given in figure 5. Note that the weight is 1 for an observation unless the Mahalanobis distance is greater than k. The weight then decreases inversely with the Mahalanobis distance. If all observations are sufficiently well-behaved, then all the weights remain 1 and the ordinary estimates result.

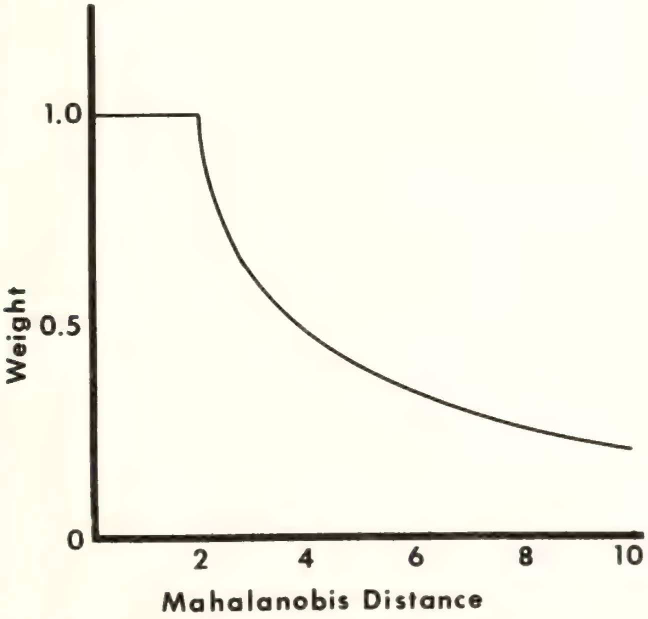

Figure 5. Weight function for estimating the mean vector and covariance matrix by Huber's method with a constant of k = 1.97.

This approach of robust estimation can be fruitfully applied in principal component analysis, factor analysis, regression, discriminant analysis, etc. The application in this paper will be in principal components and discriminant analysis.

The robust discriminant problem is discussed in Randles et al. (1978). They discuss several procedures for the two-group case. A method that is suggested naturally is to estimate the mean vector and covariance matrix separately and robustly (as above) for each group. These are then substituted into the linear or quadratic discriminant function.

Let $\underline{x}_1, \underline{x}_2, \ldots, \underline{x}_n$ and $\underline{y}_1, \underline{y}_2, \ldots, \underline{y}_m$ be two independent random samples from p-variate populations. Let $\underline{z}$ be an observation from one or the other population. The Huberized linear discriminant function (HLDF) then is

$\underline{D}^*_L(\underline{z})=[\underline{z}- 1/2(\underline{\bar{x}}^*+\underline{\bar{y}}^*)]'\ \underline{S}^{*-1}_p[\underline{\bar{x}}^*-\underline{\bar{y}}^*]$ where $\underline{x}^*$ and $\underline{y}^*$ are the robust sample mean vectors and $\underline{S}^*_p$ is the robust pooled sample covariance matrix. It is defined by

$$\underline{S}^*_p = [(n-1)\underline{S}^*_x+(m-1)\underline{S}^*_y]/(n+m-2)$$

where $\underline{S}^*_x$ and $\underline{S}^*_y$ are the robust sample covariance matrices. The robust sample discriminant coefficients are given by

$$\hat{\underline{\beta}}^* = \underline{S}^{*-1}_p(\underline{\bar{x}}^*-\underline{\bar{y}}^*).$$

Fisher's linear discriminant function (LDF) is defined similarly except that the ordinary estimates are placed in the above HLDF. Huberized or Fisherian quadratic discriminant functions can be defined easily as in Randles et al. (1978).

The geometry of robust discriminant analysis is similar to that of ordinary discriminant analysis. Concentration ellipsoids are determined by the equations of the form

$$(\underline{x}-\underline{\bar{x}}^*)'\underline{S}^{*-1}_p(\underline{x}-\underline{\bar{x}}^*) = c \text{ and}$$

$$(\underline{y}-\underline{\bar{y}}^*)'\underline{S}^{*-1}_p(\underline{y}-\underline{\bar{y}}^*) = c$$

where c is a positive constant. Probability statements can be made concerning the ellipsoids by using a chi-square distribution with p degrees of freedom as an approximation.

Stability of the Estimators

In order to assess the discriminant model it is important to assess the stability of the sample discriminant coefficients. A technique both for obtaining new estimates and for assessing their stability is the Jackknife (Mosteller and Tukey 1977). An initial step of the Jackknife procedure called "leave-one-out" is also useful for validating the model. These procedures are not applied to the principal component coefficients in this paper although it would be possible to jackknife them.

The robust discriminant coefficients are given by $\underline{\hat{\beta}}^{*\prime} = (\hat{\beta}^*_1, \hat{\beta}^*_2, \ldots, \hat{\beta}^*_p)$. The method starts by recomputing the coefficients each time after leaving out a single observation. For simplicity, let j range from 1 to N=n+m whereas i=1,2,...,p denotes the variables, i.e. $\hat{\beta}^*_{i(-j)}$ is the coefficient for the ith variable with the jth observation removed. $\underline{\hat{\beta}}^*_{(-j)}$ is used to predict the jth observation in the leave-one-out validation. Note that a prediction is being made based on values which were not used in building the model.

The jth pseudo-value for variable i is given by

$$\tilde{\beta}^*_{i(-j)} = N\hat{\beta}^*_i-(N-1)\hat{\beta}^*_{i(-j)} .$$

Then the jackknife estimator is given by

$$\tilde{\beta}^*_i = \sum_{j=1}^{N} \tilde{\beta}^*_{i(-j)}/N .$$

A standard deviation estimate for both $\hat{\beta}^*_i$ and $\tilde{\beta}^*_i$ is given by

$$s_{\tilde{\beta}^*_i} = \{ \sum_{j=1}^{N} (\tilde{\beta}^*_{i(-j)}-\tilde{\beta}^*_i)^2/[N(N-1)]\}^{1/2} .$$

We can then test for significance since $\hat{\beta}^*_i/s_{\tilde{\beta}^*_i}$ or $\tilde{\beta}^*_i/s_{\tilde{\beta}^*_i}$ has an approximate t distribution with N-1 degrees of freedom under the null hypothesis that the coefficient is zero (Tukey 1958).

SPARROW EXAMPLE

Since 1976 data on sparrow habitats have been collected on "reclaimed" strip mines in northern West Virginia. Our purpose is to illustrate the robust procedures discussed in the previous section using a small portion of these data. In particular, habitat data of savannah sparrows (*Passerculus sandwichensis*) and grasshopper sparrows (*Ammodramus savannarum*) areused based on field work done in 1978 on the Great Mine (47.5 ha) in Preston County, West Virginia.

Ten vegetation variables were measured based on the territories of the sparrows. However, after preliminary screening, only four variables are used in this paper. They are bare ground cover (BGC), litter depth (LD), vertical diversity of grass (VH), and total grass density (TD). Methods of measurement are described by Whitmore (1979). Units of measurement are presented only in table 1. (Tables follow literature cited.) Twenty savannah sparrows and 51 grasshopper sparrows were found on this mine in 1978. However, in order to make the sample sizes equal (for convenience) only the first 20 grasshopper sparrows were used. No attempt was made to screen the data to pick the "best" observations to illustrate our techniques.

Principal Component Analyses

The effects of outliers on principal component analyses depend on their position relative to the "ellipsoidal" swarm of points in p-space. The general effect is to shift and stretch the ellipsoid in the direction of the outliers. If the outliers are along the major axes, then the ellipsoid is elongated more than it should be. On the other hand, if the outliers are orthogonal to the major axes, the ellipsoid is contracted more than it should be.

The analyses that follow estimate the mean vectors and covariance matrices by ordinary maximum likelihood (ML) adjusted to be unbiased and by Huber's method at cutoffs of k = 1.97 (H197) and k = 1.56 (H156). The cutoff at 1.97 corresponds to weighting observations less which fall in the outer 10 percent of the distribution whereas the 1.56 cutoff corresponds to those observations in the outer 30 percent of the distribution. For this data set the 1.97 cutoff should be adequate to protect against the bad effects of outliers.

The raw data are presented in table 1 and weights based on the Huber technique in table 2. The savannah sparrow data is typical of most data sets in having a few observations (about 10%) somewhat distant from the bulk, particularly observations 16 and 17. Three values are relatively bad for the grasshopper sparrow data, observations 1, 3, and 13 (table 2).

Savannah Sparrow

Summary statistics for habitat variables measured on savannah sparrows are given in table 3. The robust mean estimates were rather similar to the ML estimates although some shift is present. The robust estimate for BGC increased relative to the ML estimate, whereas the robust mean estimates for LD, VH and TD decreased (table 3). The standard deviations estimated by H197 decreased relative to those estimated by ML, except for VH. The H156 standard deviations are consistently larger than the H197 standard deviations.

The most pronounced effect caused by outlying values was on the relationships among the variables. The H197 correlation estimates were consistently less (in absolute value) than the ML estimates. The H156 estimates were not as consistent but note that the correlation between BGC and VH is essentially zero (table 3).

In order to understand better the nature of the relationships, principal components were computed on the correlation matrix. The largest eigenvalue decreased as robustificaion increased, whereas the second largest eigenvalue increased (table 4). This indicates that the outlying observations, principally observations 1, 12, 16, and 17 (table 2), approximately lie along the first principal axis which causes the ellipsoid to be elongated with certain relationships accentuated and others obscured.

In all three techniques the percent of variation explained by the first two components was about 90% (table 4). The change of emphasis, however, is best seen by examining the eigenvectors (principal component coefficients). The first component contrasts BGC to the other variables in all cases. However, BGC becomes increasingly less important based on the robust estimates. For the ML technique, the second component seems to suggest a contrast between LD and TD. On the other hand, the robust second component suggests a linear combination of BGC and VH is important.

Grasshopper Sparrow

Summary statistics for the four variables measured on grasshopper sparrow habitat are given in table 5. Although the mean vector estimates for grasshopper sparrows were somewhat different than those for savannah sparrows, a nearly identical change occurred when the estimates were robustified. The same was true of sample standard deviations although not always with the same variables (tables 3 and 5).

For the most part, the grasshopper sparrow ML correlations were lower in absolute value than the corresponding Savannah sparrow correlations. The H197 estimates consistently indicated less strong relationships, particularly between BGC and VH. In all cases, the correlation between LD and TD remained about the same.

Results of the principal component analyses for grasshopper sparrows were analogous to those for savannah sparrows. The first two components explained about 85% of the variation with increasing importance going to the second component for the robust estimates (table 6). Again, notice the decreasing importance of BGC in the first component. In the second component, LD becomes less important whereas VH becomes more important. As with the savannah sparrow data, the robust second component is primarily a linear combination of BGC and VH (table 6).

Discriminant Analysis

The next phase of the study was to examine whether or not it is possible to discriminate between savannah and grasshopper sparrow habitat based on these four variables. Tests to determine equality of covariance matrices were not done, since it is not clear how to do this for the robust estimates. However, upon inspecting the covariance matrices, the differences between them for each estimation technique did not appear to be large enough to cause concern.

Discriminant coefficients, their standard errors, and the t-values for all methods are given in table 7. None of the coefficients were significant for any of the methods. However, in all cases the variables in the LDF model were closer to significance than the corresponding variables in the HLDF (1.97) or HLDF (1.56) models. What is the reason for this? For both species, the outliers lie along the principal axis which tends to elongate the ellipsoids, perhaps resulting in an optimistic appraisal of the LDF model's ability to discriminate. However, this better discrimination can be deceiving since estimates of the coefficients are based on outliers. Outliers in another sample might appear in totally different regions resulting in a very different discriminant model.

Predictions for the LDF, HLDF (1.97) and HLDF (1.56) models are given in table 8. A value greater or equal to zero predicts the observation to be associated with a savannah sparrow whereas a value less than zero predicts the observation to be of the grasshopper sparrow type. For the LDF model 75% of the observations are classified correctly. The corresponding result for the HLDF (1.97) model is 77.5%, and for the HLDF (1.56) model it is 65% (table 8). The LDF and HLDF (1.97) models have rather similar performances with HLDF (1.56) giving poorer results. More accurate estimates of misclassification percentages, however, were obtained from the leave-one-out predictions (table 9). These give 70, 70, and 60 correct classification percentages for LDF, HLDF (1.97), and HLDF (1.56), respectively.

We would not recommend the use of the LDF model, however, due to its dependence on outliers; the HLDF (1.97) model does as well and is more stable. As mentioned before, these data are reasonably typical with respect to outlier occurrence. Thus, a cutoff at 1.56 probably targets too many observations as outliers. This means that the HLDF (1.56) model for this data is too harsh on judging an observation to be an outlier and should not be used.

The lack of significance for the terms in the models together with the reasonably good classification indicate that models with fewer variables might discriminate nearly as well. In fact, a model based on only VH does nearly as well, but does not illustrate robustness in a multivariate setting.

Realizing that covariance matrices for each species may have been too different to justify linear discriminant analyses, ordinary and robust quadratic discriminant analyses were done. These models did not improve the probability of correctly classifying an observation and thus are not included.

REMARKS

Outliers in multivariate data are difficult to detect if the dimensionality of the space is greater than two. It is rare that practitioners of multivariate methods attempt to adjust their analyses to minimize these effects. Partly this is due to both the unavailability of techniques to deal with multivariate outliers and the lack of computer programs. Nonetheless, outliers can have pronounced effects on the conclusions.

We suggest that both classical and robust analyses be performed on the data. If they give similar results, then use the results from the classical analysis and merely note that the robust analysis was done. If the analyses give different interpretations, it is important to understand what observations caused the discrepancies. The robust analysis then is generally to be preferred.

The M-estimation technique presented in this paper is a natural extension of maximum likelihood estimation. In fact, it is just a weighted version in which the weights are determined iteratively from the Mahalanobis distances. Thus, these robust estimators are easy to understand and interpret.

Lack of computer programs will make it difficult to perform these analyses at the present time. However, the senior author is currently developing a multivariate data analysis package. Some of these procedures should be published in the SUGI (SAS User's Group International) proceedings in 1981.

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Table 1. Measurements of four habitat variables for savannah and grasshopper sparrows.[1]

	Savannah sparrow				Grasshopper sparrow			
Obs	BGC	LD	VH	TD	BGC	LD	VH	TD
1	24.3	1.02	0.98	897	19.8	6.95	1.21	899
2	36.4	1.45	0.74	449	38.7	1.20	0.57	174
3	19.1	1.02	1.00	579	4.5	3.55	0.87	364
4	42.5	0.26	0.89	197	55.0	0.47	0.54	133
5	58.4	0.18	0.56	113	33.0	2.87	0.60	418
6	15.3	1.97	1.04	432	0.5	2.95	0.73	714
7	48.8	0.27	0.52	145	33.0	0.51	0.71	222
8	50.0	0.47	0.64	212	20.5	2.41	0.79	743
9	18.0	3.31	0.83	830	22.3	0.34	0.81	188
10	44.4	2.67	0.88	381	10.5	2.00	0.83	454
11	20.0	3.15	1.14	826	24.9	1.18	0.77	404
12	14.8	1.18	0.77	859	55.5	0.53	0.61	95
13	13.4	3.10	0.92	604	66.1	0.56	0.00	154
14	40.4	0.53	0.44	210	22.9	0.48	0.32	274
15	10.6	2.60	1.00	480	20.5	1.66	0.51	308
16	0.7	6.30	1.30	1208	24.3	1.20	0.45	271
17	11.3	4.46	0.92	468	14.2	1.76	1.21	629
18	68.5	0.87	0.84	120	22.0	2.77	0.57	431
19	1.4	3.55	1.31	1090	58.5	0.41	0.56	127
20	13.7	2.42	1.07	810	14.2	2.31	0.50	451

[1] Variables are BGC - bare ground cover (%); LD - litter depth (cm); VH - vertical diversity of grass (Shannon-Weaver index); and TD - total grass density (hits/unit transect).

Table 2. Final weights for each four-variate observation using Huber's robust procedure with cutoffs of 1.97 and 1.56.

	Final Weights			
	Savannah sparrow		Grasshopper sparrow	
Obs	H197	H156	H197	H156
1	0.786	0.537	0.319	0.271
2	1	1	1	1
3	1	0.736	0.495	0.335
4	0.960	0.640	1	0.987
5	1	0.986	1	0.887
6	0.924	0.648	0.871	0.608
7	1	1	1	1
8	1	1	0.650	0.449
9	0.964	0.639	0.814	0.604
10	1	0.900	1	0.984
11	1	1	1	1
12	0.757	0.540	1	0.888
13	1	1	0.479	0.328
14	1	1	0.926	0.726
15	1	0.765	1	1
16	0.534	0.408	1	1
17	0.679	0.471	0.651	0.487
18	0.800	0.802	1	1
19	1	0.780	1	0.906
20	1	1	1	1

Table 3. Sample mean vectors, standard deviations, and correlations for four variables measured on savannah sparrow habitat using maximum likelihood and Huber's robust procedure with cutoffs of 1.97 and 1.56.

	Sample mean vectors			
	BGC	LD	VH	TD
ML	27.60	2.039	0.890	545.5
Huber (1.97)	28.13	1.940	0.880	530.6
Huber (1.56)	29.63	1.880	0.866	510.6
	Sample standard deviations			
ML	19.50	1.625	0.235	334.4
Huber (1.97)	19.16	1.325	0.248	301.2
Huber (1.56)	23.14	1.329	0.328	309.7

	Sample correlations					
	BGC vs LD	BGC vs VH	BGC vs TD	LD vs VH	LD vs TD	VH vs TD
ML	-0.728	-0.724	-0.831	0.715	0.699	0.761
Huber (1.97)	-0.715	-0.500	-0.757	0.608	0.698	0.723
Huber (1.56)	-0.421	0.032	-0.441	0.693	0.780	0.767

Table 4. Sample eigenvalues and eigenvectors based on correlation matrices for four variables measured on savannah sparrow habitat using maximum likelihood and Huber's robust procedure with cutoffs of 1.97 and 1.56.

Sample eigenvalues

	Component			
Estimator	1	2	3	4
ML	3.230	0.326	0.283	0.160
(Cum. Percent)	80.8	88.9	96.0	100.0
H197	3.007	0.516	0.311	0.166
(Cum. Percent)	75.2	88.1	95.8	100.0
H156	2.641	1.028	0.234	0.097
(Cum. Percent)	66.0	91.7	97.6	100.0

Sample eigenvectors

Estimator	Component	BGC	LD	VH	TD
ML	1	0.509	-0.485	-0.495	-0.510
	2	-0.360	-0.791	-0.096	0.485
	3	-0.425	0.336	-0.838	0.068
	4	-0.656	-0.160	0.211	-0.707
H197	1	0.496	-0.503	-0.468	-0.531
	2	-0.578	0.232	-0.779	-0.073
	3	-0.350	-0.812	-0.026	0.466
	4	-0.546	-0.183	0.416	-0.704
H156	1	0.292	-0.565	-0.505	-0.583
	2	-0.857	0.022	-0.515	-0.004
	3	-0.150	-0.809	0.210	0.528
	4	-0.398	-0.158	0.659	-0.618

Table 5. Sample mean vectors, standard deviations, and correlations for four variables measured on grasshopper sparrow habitat using maximum likelihood and Huber's robust procedure with cutoffs of 1.97 and 1.56.

Sample mean vectors

	BGC	LD	VH	TD
ML	28.04	1.806	0.658	372.6
Huber (1.97)	28.63	1.591	0.635	345.7
Huber (1.56)	28.99	1.569	0.630	337.6

Sample standard deviations

	BGC	LD	VH	TD
ML	18.24	1.576	0.274	227.0
Huber (1.97)	19.32	0.992	0.225	176.2
Huber (1.56)	20.84	1.048	0.276	182.7

Sample correlations

	BGC vs LD	BGC vs VH	BGC vs TD	LD vs VH	LD vs TD	VH vs TD
ML	-0.518	-0.542	-0.673	0.563	0.811	0.640
Huber (1.97)	-0.473	0.039	-0.537	0.266	0.779	0.478
Huber (1.56)	-0.171	0.381	-0.194	0.438	0.836	0.622

Table 6. Sample eigenvalues and eigenvectors based on the correlation matrices for four variables measured on grasshopper sparrow habitat using maximum likelihood and Huber's robust procedure with cutoffs of 1.97 and 1.56.

Sample eigenvalues

	Component			
Estimator	1	2	3	4
ML	2.883	0.502	0.457	0.158
(Cum. percent)	72.1	84.6	96.0	100.0
H197	2.349	1.048	0.442	0.161
(Cum. percent)	58.7	84.9	96.0	100.0
H156	2.279	1.290	0.332	0.099
(Cum. percent)	57.0	89.2	97.5	100.0

Sample eigenvalues

Estimator	Component	BGC	LD	VH	TD
ML	1	0.471	-0.506	-0.473	-0.547
	2	0.704	0.631	-0.235	0.225
	3	-0.477	0.151	-0.847	0.182
	4	-0.236	0.568	0.065	-0.786
H197	1	0.437	-0.572	-0.318	-0.617
	2	0.587	-0.082	0.801	0.078
	3	-0.641	-0.645	0.410	-0.067
	4	-0.231	0.500	0.297	-0.780
H156	1	0.025	-0.589	-0.502	-0.633
	2	0.843	-0.209	0.474	-0.148
	3	-0.479	-0.632	0.602	0.092
	4	0.245	-0.458	-0.402	0.754

Table 7. Four-variate discriminant coefficient estimates and standard errors for Fisher's linear discriminant model and Huber's robust linear discriminant models.

	LDF			
	BGC	LD	VH	TD
$\hat{\beta}$	0.0656	-0.525	5.40	0.00427
$s_{\hat{\beta}}$	0.0431	0.668	2.97	0.00282
$t_{\hat{\beta}}$	1.52	-0.79	1.82	1.51
	HLDF (1.97)			
	BGC	LD	VH	TD
$\hat{\beta}^*$	0.0249	-0.336	3.45	0.00338
$s_{\hat{\beta}^*}$	0.0303	0.655	2.45	0.00340
$t_{\hat{\beta}^*}$	0.82	-0.51	1.41	0.99
	HLDF (1.56)			
	BGC	LD	VH	TD
$\hat{\beta}^*$	-0.00402	-0.683	2.38	0.00308
$s_{\hat{\beta}^*}$	0.0294	0.682	3.09	0.00369
$t_{\hat{\beta}^*}$	-0.14	-1.00	0.77	0.83

Table 8. Discriminant predictions based on Fisher's linear discriminant model and Huber's robust linear discriminant models.

	Predictions					
	Savannah sparrow			Grasshopper sparrow		
Obs	LDF	(1.97) HLDF	(1.56) HLDF	LDF	(1.97) HLDF	(1.56) HLDF
1	3.22	2.47	2.51	1.07	1.16	-0.96
2	0.59	0.28	0.22	-1.23	-1.09	-0.88
3	1.64	1.33	1.60	-2.27	-1.05	-1.04
4	1.35	0.50	0.58	-0.11	-0.68	-0.64
5	0.29	-0.50	-0.47	-1.27	-0.87	-1.17
6	0.48	0.56	0.61	-1.48	-0.25	0.13
7	-0.47	-0.80	-0.49	-0.28	-0.36	0.10
8	0.44	-0.20	-0.14	0.56	0.73	0.65
9	0.51	0.80	0.41	-0.49	-0.34	0.39
10	0.94	0.32	-0.53	-0.90	-0.22	0.17
11	2.39	1.96	1.24	-0.06	0.04	0.38
12	1.22	1.33	1.82	0.11	-0.58	-0.63
13	-0.16	0.30	0.09	-2.26	-2.23	-1.97
14	-1.31	-1.15	-0.62	-2.81	-1.77	-0.61
15	-0.17	0.26	0.25	-2.41	-1.45	-0.85
16	1.96	2.26	0.72	-2.40	-1.54	-0.80
17	-1.59	-0.67	-1.25	2.27	1.85	1.77
18	2.13	0.51	-0.29	-2.05	-1.17	-1.09
19	3.00	2.84	2.26	0.23	-0.53	-0.58
20	1.91	1.75	1.54	-2.61	-1.38	-0.85
Misclassified	5	5	7	5	4	7

Table 9. Discriminant leave-one-out predictions based on Fisher's linear discriminant and Huber's robust linear discriminant models.

	Leave-One-Out Predictions					
	Savannah sparrow			Grasshopper sparrow		
		(1.97)	(1.56)		(1.97)	(1.56)
Obs	LDF	HLDF	HLDF	LDF	HLDF	HLDF
1	3.32	2.33	2.30	3.85	1.79	-0.37
2	0.55	0.24	0.17	-1.17	-1.01	-0.78
3	1.53	1.26	1.48	-2.13	-1.01	-0.82
4	1.17	0.23	0.33	0.08	-0.45	-0.36
5	0.07	-0.79	-0.78	-1.17	-0.55	-0.91
6	0.25	0.32	0.31	-1.32	0.01	0.29
7	-0.66	-1.08	-0.72	-0.16	-0.14	0.40
8	0.32	-0.35	-0.30	0.82	0.99	0.84
9	0.31	0.51	0.11	-0.14	0.15	0.97
10	0.76	-0.06	-0.89	-0.78	-0.01	0.49
11	2.33	2.05	1.31	0.01	0.15	0.55
12	0.83	0.88	1.47	0.36	-0.34	-0.39
13	-0.26	0.20	-0.06	-1.96	-2.49	-1.69
14	-1.64	-1.47	-0.86	-2.78	-1.53	-0.45
15	-0.43	0.04	-0.08	-2.36	-1.41	-0.80
16	1.68	1.64	0.10	-2.35	-1.47	-0.76
17	-2.72	-2.02	-2.42	3.46	2.41	2.33
18	1.92	0.18	-0.67	-1.98	-0.97	-0.83
19	3.01	3.13	2.29	0.52	-0.23	-0.29
20	1.84	1.86	1.69	-2.56	-1.24	-0.67
Misclassified	5	6	9	7	6	7

DISCUSSION

STEVEN PARREN: In addition to the elimination of outliers, does robust DFA have an advantage over transformations of habitat variables as we measure (and perceive) these variables in the field?

E. JAMES HARNER: The use of robust estimates does not preclude the use of transformations but it often makes it unnecessary to transform. An outlier can make it appear that a log (say) transform is necessary. I prefer not to transform unless absolutely necessary because of the difficulty of interpretation.

STEVEN PARREN: Are homogenous covariance matrices ever found in ecological studies?

E. JAMES HARNER: Yes, within reasonable statistical variability. In most cases, however, they are probably both biologically and statistically different. We need more research on the effect of not satisfying this assumption on the linear discriminant function. I believe A.P. Dempster (1969. Elements of continuous multivariate analysis. 388 p. Addison-Wesley, Reading, Mass.) somewhat quantifies the "difference" in covariance matrices.

STEVEN PARREN: What effects do transformations of variables used in multivariate space (DFA) have on the ecological interpretation of habitat variables?

E. JAMES HARNER: If the object is strictly classification then by using, for example, the power family of transformations causes few conceptual difficulties. However, if you desire to "interpret" the coefficients I believe it does. The robust approach can sometimes make it unnecessary to transform.

LESLIE MARCUS: Standard errors of your jackknifed coefficients are large, which support the idea that it is difficult to interpret coefficients. Please comment.

E. JAMES HARNER: The t-tests based on these standard errors are not significant, but the robust standard errors are on the whole somewhat smaller than those of the standard analysis. We did not use variable selection in determining this model. In order to complete the model-building process, it would be necessary to eliminate one or more variables from the discriminant analysis to remove the redundancies.

USE OF DISCRIMINANT ANALYSIS AND OTHER STATISTICAL METHODS IN ANALYZING MICROHABITAT UTILIZATION OF DUSKY-FOOTED WOODRATS[1]

Janet I. Cavallaro[2], John W. Menke[3], and William A. Williams[4]

Abstract.--In the past 10 years, discriminant analysis has become an increasingly used statistical method in small mammal studies. Although originally developed as a classification procedure, it has been used by ecologists and wildlife biologists for a variety of other purposes. No generally accepted methods, however, have been developed for interpreting the discriminant functions used for these alternative purposes.

Using the dusky-footed woodrat (Neotoma fuscipes) as an example, we present a method for interpreting discriminant functions when the purpose is both to characterize microhabitats used by a species and to explain why individuals of a species occur in some microhabitats and not in others. Three types of discriminant functions were identified from which hypotheses of different forms were developed. More complete interpretation of two-group discriminant functions can be made if a multiple regression is calculated for the dependent variable, presence or absence of woodrats and if partial correlations are calculated for the independent variables. Since multiple regression coefficients are unstable if multicollinearity exists among the independent variables, the variance inflation factor was calculated and ridge regression was performed so that the effect of intercorrelated variables could thereby be examined and unstable variables eliminated wherever necessary.

Key words: California chaparral; multicollinearity; multiple regression; partial correlation; ridge regression; variance inflation factor; wildlife habitat analysis.

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INTRODUCTION

Discriminant analysis was developed as a classification procedure for assigning unknown specimens to one of two or more groups. In small mammal studies, however, discriminant analysis has also been used for other purposes: 1) evidence of niche separation, 2) hypothesis formulation about the mechanism of coexistence of sympatric species, and 3) characterization of microhabitats.

M'Closkey (1976) and Holbrook (1978) used discriminant analysis to provide evidence of niche separation of small mammal species by equating structural variables in discriminant functions to niche dimensions that separated the niches of small mammal species. M'Closkey recommended caution in equating statistical and biological patterns of microhabitat use, but then went on to suggest that

> "the statistical patterns of separation reflect ecological and evolutionary adjustments to inter-specific competition. Structural habitat division by rodents is either the means by which co-existence is achieved or is correlated with other niche dimensions (e.g., food) responsible for coexistence."

Unless hypotheses are developed from the discriminant function to explain how species partition the habitat according to structural variables, however, little new insight is achieved.

In other work, M'Closkey and Fieldwick (1975) used discriminant analysis to develop hypotheses to explain how two sympatric species could coexist. They hypothesized that since the discriminant function contained structural habitat variables that were characteristic structural features of optimal habitats of Microtus pennsylvanicus or Peromyscus leucopus, the two species were sympatric because animals of each species could find microhabitats which corresponded to their optimal habitat. They observed that foliage height diversity and tree basal area in Peromyscus microhabitats were respectively 1.5 and 4 times greater than in Microtus microhabitats, and the depth of the grassmat in Microtus microhabitats was twice as deep as in the Peromyscus microhabitats.

Dueser and Shugart (1978) used discriminant analysis to characterize the microhabitats of small mammal species and to explain why individuals of a species occurred in some microhabitats and not in others. By restricting their analysis to significant univariate variables they were able to conclude that species X occurred where more of habitat variable A occurred, where habitat variable B was larger, and so forth. They used the simple correlation between the function and each variable in the function to measure the "relative contribution of the variable to the power of the function to discriminate between groups". Simple correlation coefficients, however, are inappropriate whenever more than one independent variable is involved since they only show which univariate variables would separate the groups similarly to the function. The relative magnitude of the correlation coefficient corresponds exactly to relative value of the univariate F-ratios (Marascuilo and Levin[5]).

Using live-trap data collected on dusky-footed woodrats in chamise-wedgeleaf ceanothus (Adenostoma fasciculatum-Ceanothus cuneatus) chaparral in northern California, we present a method for interpreting discriminant functions that includes: 1) determination of the type of discriminant function to be used, 2) assessment of multicollinearity with the variance inflation factor and ridge regression, 3) use of multiple regression and partial correlation analysis, and 4) development of hypotheses to explain why individuals of a species frequent some microhabitats and not others.

FIELD METHODS

Woodrats were trapped on 0.5-ha and 1.0-ha grids in 14- and 25-year old chamise-ceanothus chaparral, respectively, for periods of 6 nights. Fifty-two structural, botanical, and physical habitat variables describing each microhabitat were measured using point sampling and nearest neighbor methods (Cavallaro 1978).

INTERPRETING DISCRIMINANT FUNCTIONS

Discriminant functions can serve as the basis for characterizing habitats used by individuals of a species. The characterization, however, is much more useful if researchers hypothesize why a species uses habitats with particular characteristics. Partial correlation analysis can assist in hypothesis development. Hereafter, we present our approach to interpreting discriminant functions in wildlife habitat studies using the woodrat as an example.

Selection of Discriminant Function Type

We have identified three types of discriminant functions that help both to characterize the habitats used by a species and to generate hypotheses explaining that habitat use. The types are distinguished on the basis of whether or not the function contains variables which as univariate variables identify a difference between where individuals of a species do and do not occur. The three types of functions are as follows: Type I contains only significant univariate variables, Type II contains both significant and nonsignificant univariate

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[5] Textbook in preparation, Marascuilo, L.A., and J. Levin, Department of Education, University of California, Berkeley.

Table 1. Variables included in two discriminant functions that separated trap sites used and not used by dusky-footed woodrats on the 14- and 25 year-old plots; also shown are univariate statistics and variance inflation factors.

Variable	Discriminant function type	Univariate		Variance inflation factor	
		F	R^2	DF Type I	DF Type II
14-year-old plot					
1. Other shrub species density	I, II	**	0.175	0.4	121.4
2. Other shrub species live leaf density	I	**	0.135	3.4	
3. Other shrub species live stem density	I, II	**	0.197	15.5	116.0
4. Other shrub species dead stem density	I	**	0.159	10.1	
5. Chamise dead stem density	I	**	0.136	2.8	
6. Chamise density	I, II	*	0.099	2.8	2.0
7. Total vegetation cover	II		0.004		1.7
8. Vertical canopy density 100-150 cm aboveground	II		0.021		3.0
9. Vertical canopy density 150-200 cm aboveground	II		0.009		2.0
10. Total stem (< 0.5 cm in diameter) density	II		0.022		2.3
11. Ceanothus live leaf density	II		0.007		1.4
12. Yerba santa live leaf density	II		0.026		1.1
Type I discriminant function**, $R^2 = 0.29$					
Type II discriminant function**, $R^2 = 0.53$					
25-year-old plot					
13. Other ground cover	I, II	**	0.103	1.1	1.2
14. Live stem (< 0.5 cm in diameter) density	I, II	*	0.070	1.1	1.2
15. Live stem (1.0-2.5 cm in diameter) density	I, II	*	0.064		
16. Chamise live leaf density	I, II	*	0.068	1.1	7.1
17. Vertical canopy density 0-2.5 cm aboveground	II		0.016		1.2
18. Live leaf density	II		0.026		6.7
19. Total stem (0.5-1.0 cm in diameter) density	II		0.043		1.1
Type I discriminant function**, $R^2 = 0.21$					
Type II discriminant function**, $R^2 = 0.40$					

*P < 0.05, **P < 0.01

variables, and Type III contains only nonsignificant univariate variables. Hypotheses based on Type I discriminant functions would state that where woodrats occur variables x, y, and z, respectively, are less, greater, and less than where woodrats do not occur for some proposed reason. In contrast, hypotheses based on Type III discriminant functions would state that where woodrats occur X = value D, Y = value E, and Z = value F, and this particular combination of variable values is important for some proposed reason even though similar values of x, y, and z can be found in microhabitats not used by woodrats. Hypotheses based on Type II discriminant functions would state that where woodrats occur variable X is greater, Y = value H, and Z = value I for a stated reason which must explain why more of X is necessary and why variables Y and Z have their particular values even though similar values of Y and Z can be found in microhabitats not used by woodrats.

It becomes apparent that hypotheses developed from Type II or III discriminant functions are much more difficult to justify because the functions would indicate that animals are using extremely specific microhabitats. Those discriminant functions may often have questionable ecological significance. For comparison, however, we will include Type I and II discriminant functions in our discussion.

If a satisfactory hypothesis can be developed from a Type I discriminant function, selection of variables is a simple matter. All significant univariate variables are used. Selection of variables to include in a Type II or Type III discriminant function is more difficult. A useful strategy is to use those variables that increment the coefficient of determination, R^2, by a specified minimum amount (Marascuilo and Levin[5]); we used a 2% increment for Type II and III discriminant functions.

Discriminant Functions

For the 14-year-old plot, the Type I discriminant function had a R^2 value of 29% and contained all significant univariate variables except one, other shrub species live leaf density (2) (table 1). The Type II discriminant function had a R^2 value of 53% and contained in addition to all nonsignificant univariate variables listed in table 1 three density variables, other shrub species (1), other shrub species live stems (3), and chamise (6). For the 25-year-old plot, the Type I discriminant function had a R^2 value of 21% and contained all significant univariate variables. The Type II discriminant function had a R^2 value of 40% and contained all nonsignificant univariate variables listed in table 1 as well as all significant univariate variables.

The coefficient of determination, R^2, is considered a useful statistic because a function may be significant and yet very little variation in the function may be associated with the variables in the discriminant function. In such cases, the function contributes little information. In the field of educational psychology, R^2 values less than 10% are considered too inconsequential to be reported.[6]

Knowing the importance of each variable in the discriminant functions would be extremely useful for developing hypotheses. Fortunately, the two-group case of discriminant analysis can be done as a multiple regression, with the dependent variable being presence or absence of woodrats; and thereafter, partial correlations can be calculated to assess the importance of habitat variables. Partial correlations are a measure of association between each independent variable and the dependent variable in the multiple regression.

Assessment of Multicollinearity in Multiple Regression

In data sets containing measurements of uncontrolled variables, as is usually the case in wildlife habitat studies, multicollinearity often exists among variables and can cause ambiguous results in ordinary multiple regression (Hoerl and Kennard 1970). Resulting regression coefficients can be inflated in absolute value or may even have the wrong sign. The possibility that such difficulties will occur increases as independent variables diverge from orthogonality. Thus, it is desirable to test for multicollinearity among independent variables.

Calculation of the variance inflation factor (VIF) is the preferred method for determining whether a multicollinearity problem exists, because the VIF will detect relations that exist among several variables that might not be evident from examination of simple correlations (Williams et al. 1979). VIF equals $1/(1-R_i^2)$ where R_i^2 is the multiple correlation coefficient of one independent variable with all other independent variables. As R_i^2 approaches 0 (orthogonality) VIF approaches 1; whereas, as R_i^2 approaches 1 (variables are highly intercorrelated) VIF approaches infinity. VIF values exceeding 10 are considered likely to cause problems in estimating regression coefficients (Chatterjee and Price 1977). "Tolerance" is the reciprocal of the VIF, and the equivalent critical value is 0.1.

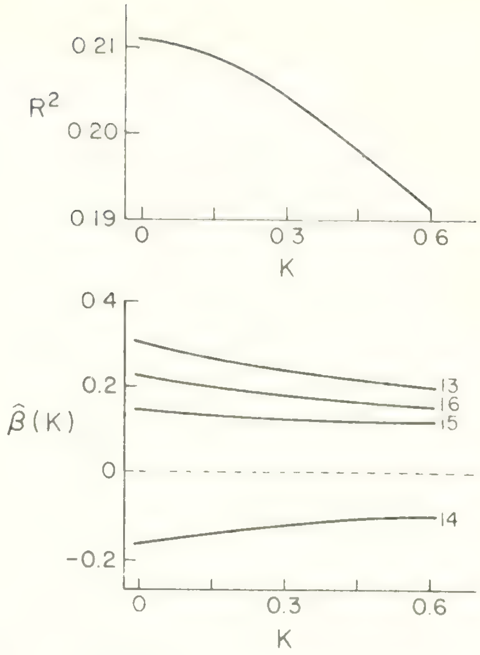

Figure 1. **Ridge trace for variables in the Type I** discriminant function for the 25-year-old plot. Variables as defined in table 1.

One or more variables in the two discriminant functions for the 14-year-old plot has a VIF value which exceeds 10, suggesting that for those variables the regression coefficients probably are not stable (table 1). In contrast, neither function for the 25-year-old plot contained any variables with a VIF greater than 10, thus all those variables can be used in calculating a multiple regression and partial correlations.

Ridge regression was developed to alleviate problems from intercorrelated independent variables by including a bias factor k when regression coefficients are estimated (Hoerl and Kennard 1970). The first step in ridge regression involves making a ridge trace by adding increments of k over the range of 0 to 1 and plotting the respective standardized partial regression coefficients $\hat{\beta}(k)$ against k. As k increases the coefficient of determination, R^2, decreases.

The ridge trace for variables contained in the Type I discriminant functions for the 25 year-old plot (fig. 1) shows that the regression coefficients are stable as would be expected since no variables in that discriminant function had a VIF value greater than 10. As k increases, the standardized regression coefficients $\hat{\beta}(k)$ maintain both their absolute value and their values relative to each other quite well. In contrast, in the ridge trace for variables contained in the Type I discriminant function for the 14 year-old plot (fig. 2) variables 2 and 4, other shrub species live leaf density and other shrub species dead stem density, were negative for $k = 0$ and became positive for $k > 0.13$, indicating that those variables are highly unstable. Variable 3, other shrub species live stem density, was high and positive at $k = 0$, but decreased rapidly as k increased, suggesting that variable 3 is also unstable.

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[6] Personal communication with L.A. Marascuilo, Professor of Statistics, Department of Education, University of California, Berkeley.

The ridge trace shows either what k value to use, if a multiple regression is desired for a particular combination of variables (a value which stabilizes the regression coefficients while not greatly decreasing the R^2 value), or which variables to eliminate because they are unstable. The ridge trace shows visually what the VIF values suggest.

Variables lacking stability were eliminated from the Type I discriminant function for the 14-year-old plot leaving other shrub species live stem density (3) and chamise dead stem density (5). Both had a VIF of 1.3 and stable regression coefficients upon calculation (fig. 3).

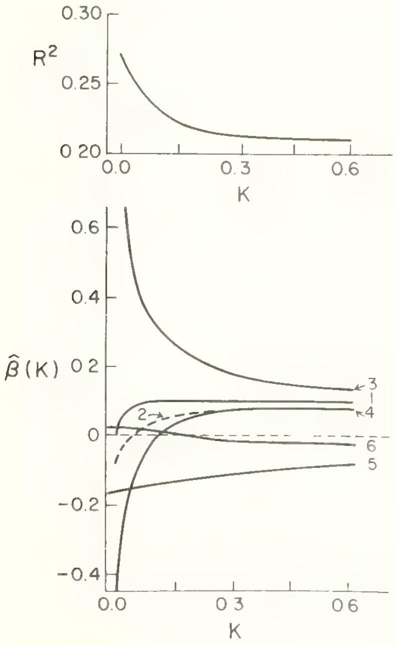

Figure 2. Ridge trace for variables in the Type I discriminant function for the 14-year-old plot. Variables are defined in table 1.

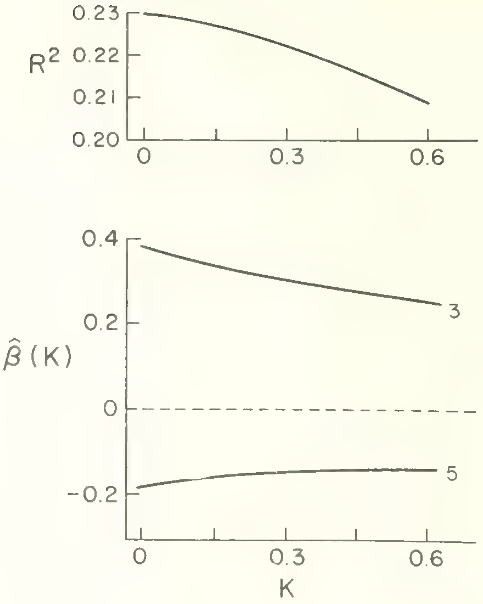

Figure 3. Ridge trace for variables originally in the Type I discriminant function for the 14-year-old plot which remained after assessing intercorrelation among variables. Variables are defined in table 1.

The ridge trace for variables in the Type II discriminant function for the 14-year-old plot is shown in figure 4. Variable 1, other shrub species density, was strongly negative for $k = 0$ but became positive for $k > 0.06$. In contrast, variable 3, other shrub species live stem density was strongly positive for $k = 0$ but decreased rapidly in value for $k > 0$. For $k = 0$ these two variables had opposite signs, even though they had a simple correlation of 0.99 and therefore represent the same underlying variable. These results demonstrate how multicollinear variables can greatly affect the stability of regression coefficents. After eliminating two variables in the Type II discriminant function, the VIF for all variables was less than 3.0, and a new ridge trace of the restricted variables show that the variables were much more stable (fig. 5).

Microhabitat Use Hypotheses

Based on the Type I discriminant function for the 14 year-old plot, microhabitats used by woodrats can be characterized generally as having greater density of other shrub species and lesser density of chamise, and specifically as having greater density of live leaves, live stems, and dead stems of other shrub species and less density of dead chamise stems, than microhabitats not used. This combination of variables was associated with 29% of variability in woodrat occurrence (table 1 and 2). The reason woodrats occur in these microhabitats can be hypothesized from partial correlation coefficients. Although a correlation does not prove cause and effect, it does suggest variables to consider in trying to establish a cause and effect relationship. A positive relationship exists between woodrat presence and amount of live stems of other shrub species which included deerbrush (Ceanothus integerrimus), scrub oak (Quercus dumosa), poison oak (Toxicodendron radicans), and toyon (Heteromeles arbutifolia) with scrub oak being by far most abundant. In contrast, no relationship existed between woodrat presence and amount of dead chamise stems. We, therefore, suggest that woodrats occurred in particular microhabitats because of presence of other shrub species, rather than because of lesser amounts of chamise. This hypothesis agrees with the observation that oak species are the most important variable in determining presence of dusky-footed woodrats (Linsdale and Tevis 1951).

Based on the Type II discriminant function for the 14-year-old plot, microhabitats used by woodrats can be characterized generally as having greater density of other shrub species and less density of chamise, and specifically as having greater density of live stems of other shrub species, total vegetation cover of 80.9%, vertical canopy density of 0.6 and 0.0, respectively, for layers between 100-150 cm and between 150-200 cm above the ground, total density of 1.5 for stems less than 0.5 cm in diameter, and density of live leaves of 0.1 and 0.0 respectively for ceanothus and yerba santa. In contrast, microhabitats where woodrats did not occur can be characterized as having less density of other shrub species, particularly live stems of other shrub species, greater density of chamise, total vegetation cover of 78.7%, vertical canopy density of 0.5 and 0.1, respectively, for layers between 100-150 cm and between 150-200 cm above the ground, total density of 1.7 for stems less than 0.5 cm in diameter, and density of live leaves of 0.1 and 0.0, respectively for ceanothus and yerba santa. We do not think this function provides a good characterization of microhabitats used and not used by woodrats because we can give no reason why woodrats would select such specific microhabitats. Why, for example, should they distinguish between 80.9 and 78.7% total vegetation cover, and so forth? Consequently, we suspect that the Type II discriminant function has statistical significance in this case but lacks ecological validity.

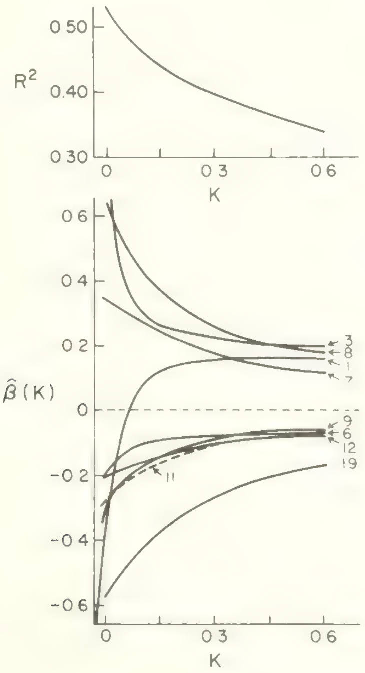

Figure 4. Ridge trace for variables in the Type II discriminant function for the 14-year-old plot. Variables are defined in table 1.

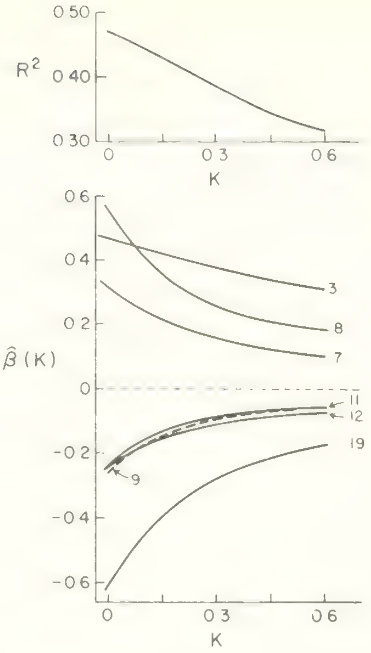

Figure 5. Ridge trace for variables originally in the Type II discriminant function for the 14-year-old plot which remained after assessing the intercorrelation among the variables. Variables are defined in table 1.

On the 25-year-old plot, where other shrub species were essentially absent (they accounted for only 1.5% of the shrub cover in contrast to 6% on the 14-year-old plot) and where all other species shrub cover was produced by deerbrush, woodrats did not occur in microhabitats with greater density of other shrub species. On the 25-year-old plot, they occurred instead where more other ground cover was present, density of live chamise leaves was greater, density of live stems between 1.0 and 2.5 cm in diameter was greater, and density of live stems less than 0.5 cm in

Table 2. Mean values (percent) for all variables in Type I and II discriminant functions and partial correlations for variables in Type I and II multiple regressions for the 14- and 25-year-old plots.

Variable	Microhabitat		Partial
	Used	Not Used	Correlation
----------14-year-old plot----------			
Type I discriminant function			
1. Other shrub species density	0.6	0.0	
2. Other shrub species live leaf density	0.1	0.0	
3. Other shrub species live stem density	0.2	0.0	0.33**
4. Other shrub species dead stem density	0.3	0.0	
5. Chamise dead stem density	0.6	0.9	-0.20
6. Chamise density	1.4	2.1	
Type II discriminant function			
1. Other shrub species denisty	0.6	0.0	
3. Other shrub species live stem density	0.2	0.0	0.48**
6. Chamise density	1.4	2.1	
7. Total vegetation cover	80.9	78.7	0.30*
8. Vertical canopy density 100-150 cm aboveground	0.6	0.5	0.41**
9. Vertical canopy density 150-200 cm aboveground	0.0	0.1	-0.28**
10. Total stem (<0.5 cm in diameter) density	1.5	1.7	-0.53**
11. Ceanothus live leaf density	0.1	0.1	-0.30*
12. Yerba santa live leaf density	0.0	0.0	-0.33*
----------25-year-old plot----------			
Type I discriminant function			
13. Other ground cover	2.1	0.3	0.28**
14. Live stem (<0.5 cm diameter) density	0.2	0.5	-0.20
15. Live stem (1.0-2.5 cm in diameter) density	0.1	0.0	0.11
16. Chamise live leaf density	0.5	0.3	0.20
Type II discriminant function			
13. Other ground cover	2.1	0.3	0.32**
14. Live stem (<0.5 cm in diameter) density	0.2	0.5	-0.29**
15. Live stem (1.0-2.5 cm in diameter) density	0.1	0.0	0.23*
16. Chamise live leaf density	0.5	0.3	0.31**
17. Vertical canopy density 0-25 cm aboveground	0.2	0.3	-0.43**
18. Live leaf density	0.7	0.5	-0.25*
19. Total stem (0.5-1.0 cm in diameter) density	0.1	0.0	0.31**

*$P < 0.05$, **$P < 0.01$

diameter was less. This combination of variables was associated with 21% of the variability in woodrat occurrence (tables 1 and 2).

The only significant partial correlation between woodrat presence and a habitat variable was for amount of other ground cover. Other ground cover consisted mainly of large downed branches which might have attracted the woodrats. Linsdale and Tevis (1951) stated: "Every pile of dead wood within the rat habitat eventually receives an accumulation of twigs deposited by the rats."

Since no significant partial correlation existed between woodrat presence and any other habitat variable and since we cannot explain why other habitat variables in the Type I discriminant function would be particularly important to woodrats, we hypothesize that other significant differences between where woodrats occurred were the result of woodrat activity in their microhabitats rather than because woodrats select microhabitats with those particular characteristics. The lower density of live stems less than 0.5 cm in diameter may have resulted from woodrat utilization of the vegetation. Woodrats cut the terminal branches of chamise and wedgeleaf ceanothus and take them to their houses where they feed on leaves and flowers (Linsdale and Tevis 1951). This continual pruning of the plants may cause improved vigor so that a greater density of live chamise leaves and a greater density of live stems between 1.0 cm and 2.5 cm in diameter occur in microhabitats used by woodrats. In this habitat dominated by mature chamise and wedgeleaf ceanothus plants, it appears, then, that woodrat selection of microhabitats may have been in response to other ground cover, while other significant differences between where woodrats did and did not occur were the result of woodrat activity.

The Type II discriminant function for the 25 year-old plot contained four significant and three nonsignificant univariate variables. Again, we could not explain why woodrats would select microhabitats with such specific densities of live leaves, stems between 0.5 cm and 1.0 cm in diameter, or a vertical canopy density between 0 cm and 25 cm above ground, and therefore concluded that this combination has little ecological validity even though more of the variation in woodrat presence was associated with that combination of variables. The combination of variables probably only had statistical significance.

CONCLUSIONS

Discriminant analysis, multiple regression, and partial correlation results can be used together to characterize the microhabitats used by individuals of a species and to generate hypotheses explaining why animals occur in some microhabitats and not in others. The specific form of the hypothesis will vary depending on the type of discriminant function.

If the habitat variables are highly multicollinear, however, estimates of the regression coefficients are unstable and unreliable. In such cases VIFs can be calculated or ridge regression can be used to identify the unstable variables for elimination prior to running the multiple regression and partial correlations.

The multivariate approaches in wildlife studies can suggest hypotheses to explain observations made by the researcher. These hypotheses should themselves then be tested so that advances can be made in our understanding of the habitat relationships of wildlife species.

ACKNOWLEDGMENTS

We thank L.A. Marascuilo for his assistance in the statistical interpretation of our data and we thank D.R. McCullough, W.E. Waters and D.E. Capen for their helpful comments on an earlier draft of our manuscript.

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DISCUSSION

LESLIE MARCUS: 1) The three types of discriminant analyses, while simpler, remind me of original suggestions in use of uncorrelated variables in physical anthropology (Pearson coefficient of racial likeness). However the type II variables may represent a "gestalt" or common habitat factor for the organism. One way of getting at that might be a rotation of the multivariate discriminant coefficient akin to oblique factor rotations, of course only reasonable for $K > 2$ groups. 2) I would suggest a better choice for your "types" would be the Mahalanobis distance d_i for each variable rather than a significance test. The "type" test is both sample size dependent and dependent on significance and level and, of course, still requires a cutoff for D. 3) I would prefer Mahalanobis D^2 as a measure of difference rather than R^2 for overall discrimination, because it gives a plottable metric in the canonical variate of discriminant space. 4) It is suggested that correlation between canonical variate and original variate be looked at. It has been shown that for two groups this is just a simple function of the mean difference (Bergmann, R.E. 1970. Interpretation and use of a generalized discriminant function. p. 35-60. In Bose, R.C. et al., editors. Essays in probability and statistics. University of North Carolina Press.) In K groups, this is not so since vectors are not orthogonal. Perhaps for full interpretation these correlations should be given; they are almost never reported.

JANET CAVALLARO: We find your comments on discriminant analysis valuable and we think that they may be very useful in further interpreting discriminant functions. In response to your fourth comment, in the two-group discriminant case, the correlation between the canonical variate and the original variables provides no new information and cannot be used in interpreting the original variables as you stated. In discriminant analysis where the number of groups exceeds two, the correlation may be useful; but it is useful only in trying to interpret what the canonical variate represents, not in interpreting the importance of the original variables in separating the groups. An original variable may be important because it separates the groups or it may be important because it in combination with the other original variables creates a new variable, the canonical variate, which separates the groups.

KEN MORRISON: In your first example, it was only for *Peromyscus maniculatus* (the most numerous species) that the discriminant function was successful. Does this really mean that the discriminant function failed?

JANET CAVALLARO: A discriminant function must be evaluated both statistically and ecologically; and although it may be significant statistically, we contend that it may be ecologically meaningless. In the case of the discriminant functions reported by Holbrook (1978), we assume that at least some of the discriminant functions must have been statistically significant, but we question whether or not they were ecologically meaningful. She provided no ecological interpretation of the functions except to infer that "species occupy habitats with characteristic three-dimensional structure". We found it surprising ecologically that the microhabitats used by *Peromyscus maniculatus* could be classified better than those used by *P. truei*, *P. boylii*, *P. dificilis*.

In our work in the chamise-ceanothus chaparral, *P. maniculatus* and *P. truei* occurred on all study plots. We could separate those microhabitats *P. maniculatus* used from those they did not use on only one of those plots. In contrast, on all the study plots, we could separate the microhabitats *P. truei* used from those they did not use. Considering the ubiquitous distribution of *P. maniculatus*, these results conform more with current understanding of the habitat relations of these species. We should mention, however, that as researchers we are searching for new information so that the discriminant functions Holbrook reported should not necessarily be negated. We believe, however, that the burden rests on her to hypothesize why the microhabitat used by *P. maniculatus* could be classifed more readily than those used by the other three species.

GERALD SVENDSEN: Because many of your measured variables are not independent from one another, do you think that you would have gained any insight by using a factor analysis to derive new composite yet independent variables and then performing multiple regression on these new variables?

JANET CAVALLARO: I think the question you are asking is whether or not principal components could have been used to create a set of independent "habitat" variables for the multiple regression analysis rather than using ridge regression to identify redundant or highly intercorrelated habitat variables. The answer is definitely yes, but the use of principal components can create problems in itself. Primarily, each principal component must be interpreted as to what it measures, and this interpretation itself can be a difficult task. By using the ridge regression to identify a set of relatively independent habitat variables, that problem is avoided.

In our approach to analyzing the data, we used the discriminant analysis to characterize the microhabitats used by a particular species and to determine how much of the variance between where a species did and did not occur could be accounted for by the combination of variables in the discriminant function. We were, therefore, interested in the suite of characters which described the microhabitats used by a species and we were not concerned about whether or not the variables were intercorrelated.

The variables in the discriminant function which characterized the species' microhabitats, however, may or may not be the variables to which the animals respond. The subsequent multiple regression and partial correlation analysis was then used to hypothesize why the animals occurred in particular microhabitats and not in others. For this phase of the analysis, however, independent habitat variables were required. We preferred ridge regression over principal components to obtain a set of independent habitat variables because, as already mentioned, we were able to use the habitat variables which were actually measured rather than using statistical habitat variables, principal components, which themselves require interpretation.

PAUL GEISSLER: If I understand what you said, the difference between the conclusions associated with the types of discriminant functions is that significant univariate variables can be interpreted individually while nonsignificant variables cannot. It seems to me that whether or not variables can be interpreted individually depends on whether or not it is correlated with other variables, and not whether or not a relationship can be demonstrated with the response variable. Also it seems to me that limiting the discriminant functions to significant variables may cause one to miss complex relationships which depend on more than one variable.

JANET CAVALLARO: The different types of

discriminant functions do not determine whether or not the individual variables in the discriminant function can be interpreted; the different types of discriminant functions determine how the individual variables must be interpreted. The discriminant function is a new "habitat" variable which is a sum of weighted habitat variables, not a response variable. If the discriminant function contains only significant univariate variables (Type I), the discriminant function can be interpreted as separating microhabitats which have more of variable X, less of variable Y, and more of variable Z from microhabitats which have less of variable X, more of variable Y, and less of variable Z. If the discriminant function contains insignificant variables as well (Type II), the discriminant function can be interpreted as above plus the fact that in microhabitats used by a particular species, variable A has a certain average value. The hypothesis generated from a Type II discriminant function, therefore, may include the idea that variable A, the insignificant univariate variable, must be at a certain threshold level before the animals of a species will use a certain habitat. If that is the case, however, a significant difference should exist in variable A between where animals do and do not occur if a broader range of habitats were sampled. Thereafter, a Type I discriminant function may well be developed to separate the microhabitats used and not used.

In our study in the chamise-ceanothus chaparral, ceanothus density did not differ between where Peromyscus truei did and did not occur on the 25-year-old plot, and yet ceanothus density was a variable in the Type II discriminant function. P. truei occurred where ceanothus density equalled 1.7 in contrast to 1.5 where P. truei did not occur. It was not clear to us why P. truei should select on the average microhabitats with a ceanothus density of 1.7 in contrast to 1.5 when those two values were essentially no different. On the 8-year-old plot ceanothus density was much less, however, and P.truei occurred where the ceanothus density was significantly greater, 1.2 in contrast to 0.2 where they did not occur. From these results on the 8- and 25-year-old plots, we can comfortably hypothesize that P. truei requires a minimum density of ceanothus before they will occupy the chamise-ceanothus habitat. This is analagous to the observations of McCabe and Blanchard (1950) who found that P. truei would not use pure stands of Baccharis pilularis but that they would use the habitat when shrubs of other species were also present. The Type I discriminant function for the 8-year-old plot enables us to develop the above partial hypothesis much more easily than did the Type II discriminant function for the 25-year-old plot.

By restricting the discriminant function to significant univariate variables, complex relationships between animals and their habitats potentially can be missed; but as we have suggested, this will depend to a large extent on the range of habitats sampled. If a broad enough range of habitats is sampled, any complex relationship should be detected through a Type I discriminant function as well as through a Type II or III discriminant function. In addition, we need to consider whether or not a Type II or III discriminant function will necessarily enable us to better detect complex relationships between habitat variables and a particular species. The Type II or III discriminant function suggests that animals are using very precisely defined habitats and so for those discriminant functions to have ecological meaning, we think the measured habitat variables must be very close measures of variables to which the animals are actually responding. We question how often variables perceived by animals when they make their habitat selection are actually measured; and we therefore question whether or not many of the Type II or III discriminant functions are not just artifacts of our sampling.

A DESCRIPTIVE MODEL OF SNOWSHOE HARE HABITAT

Kathryn A. Converse[2] and Bernard J. Morzuch[3]

Abstract.--The snowshoe hare (Lepus americanus) on the southern edge of its range in Massachusetts provided an opportunity for use of multivariate analysis to model selection of common habitat components over an extensive area during the critical winter months for comparison with preferred habitat. Ten areas were chosen for variability in their vegetation structure and composition within two ecological zones of the Berkshire Mountains in western Massachusetts. Track counts were used as indices of hare distribution and regressed on measurements of ground cover; shrub volume; shrub and sapling frequency, richness and composition; tree composition, frequency and basal area; and snow depth.

A linear regression model was used to analyze these hypothesized relationships. The technique of principal components is suggested as a method of dealing with collinearity among independent variables. Tests were performed to judge the appropriateness of pooling data from different study areas. Seemingly unrelated regression was in turn, used to analyze the possibility of mutual correlation within the error structure.

Key words: Forest habitat; Massachusetts; multicollinearity; pooling cross section data; principal components; regression analysis; seemingly unrelated regression; Snowshoe hare.

INTRODUCTION

Massachusetts has over 5 million acres of land with 3 million acres of forests classfied into 40 types. In 1971-1972, 76% of these forests contained trees greater than 12 m in height and at present 45% of the state is harvestable (MacConnell 1975). In addition to increasing forestry operations, there are continuing losses of wildlife habitat due to clearing for housing, commercial and recreational developments, and drainage and filling of wetlands. It is essential that wildlife managers become concerned with the effects of such practices and develop methods for location and description of extensive areas of wildlife habitat for game and nongame species. One possible method that addresses these issues is division of the state into ecological zones (Sczerzenie 1980).

The snowshoe hare (Lepus americanus) is diversely distributed across Massachusetts from the oak-pitch pine barrens of Cape Cod to the spruce-fir thickets of the Berkshire Mountains. Some hare may have survived transplantation from

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New Brunswick, a management plan in practice since 1919. It is assumed that survival of these hare was a function of inherent selective mechanisms for corresponding habitat components. Previous studies have shown hare to use a variety of conifer and hardwood stands of all ages, species, and interspersions. In a marginal southern range such as Massachusetts, it is difficult to specify precisely the variables to be used in a habitat model.

This paper discusses a study conducted May 1978 to March 1980 where the physical features of a variety of forest types within two ecological zones in western Massachusetts were sampled intensively. A linear regression model was used to analyze the hypothesized relationships between hare activity and selection of common habitat components during the critical winter months.

STUDY AREAS

Known hare habitat was determined through correspondence and interviews with district wildlife managers, hare hunters, and local residents. Ten research areas were chosen along a 90-km circuit through eight towns located in Berkshire, Hampshire, and Franklin counties in western Massachusetts. Five areas were chosen within each of two ecological zones--transitional (zone 1) and central Berkshires (zone 2)--designated by physiographic, vegetative, and demographic variation (Sczerzenie 1980) (fig. 1). Suitability of all areas was determined by field investigation of size, permission of private land owners, year-round road access, distance from residential or recreational disturbance, vegetation structure and composition variability, presence of browse and/or fecal pellets, and ability to census all areas on snowshoes within 24 hours.

The most recent land use inventory (MacConnell 1975) indicated that the zone 1 study areas fell within predominately hardwood forests, while zone 2 study areas were predominantely softwood forests (table 1). Forest maturity was confirmed in both zones by the 12.5-18.6 m height class and by high density, 81-100% crown closure. When the study areas were viewed separately, forest types of documented importance to the hare, e.g., spruce, became more significant. Discontinuity within habitat types was not usually reflected on land use maps, but the resulting edges provided juxtaposition of food and cover.

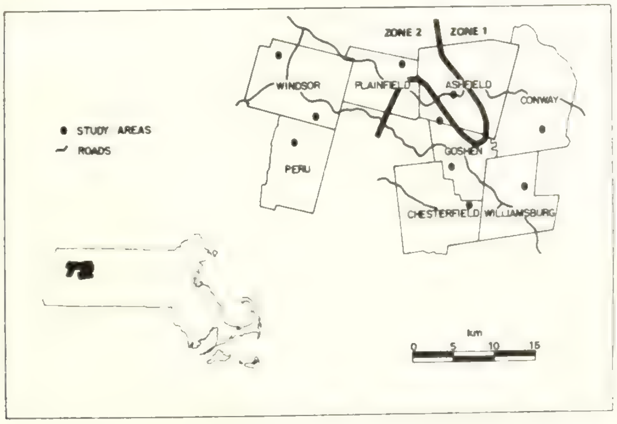

Figure 1. Location of the ten research areas within the eight Massachusetts towns and two ecological zones.

METHODS

Habitat Measurements and Hare Activity

Transect lines (total 400 m) were located randomly on each area with permanent stations every 25 m and plot centers each 50 m. Vegetation was measured September 1978 through July 1979 on all transects at each 50 m plot center. Frequency, composition, and basal area of trees 10 cm dbh and above were measured using a 10 factor prism plot. Circular plots, 40.5 m^2, were used to determine frequency, composition and richness of shrubs 30.5 cm high to 7.5 cm dbh, saplings 7.6 cm to 9.9 cm dbh, and shrub volume for mountain laurel (Kalmia latifolia) and yew (Taxus canadensis). Percent ground cover less than 30.5 cm high was visually estimated on four 2 m x 2 m quadrats and then averaged.

An understory density screen 1 m wide by 2 m high (Telfer 1974, Oldenmeyer 1975) gridded into 5% blocks was placed 15 m from and at right angles to the transect line (Nudds 1977). The screen was photographed and the lower (0-1 m) and upper (1-2 m) percent obscured by vegetation recorded as maximum density in July and minimum in March. Habitat variables used in the analyses are presented below:

RICH = number of species in the shrub and sapling plot,
EVER = evergreen trees >10 cm dbh/0.01 ha,
HARD = hardwood trees >10 cm dbh/0.01 ha,
BA = basal area m^2/ha,
SHRUB = shrub volume 100 m^3/ha,
EDBHO = evergreen stems >30.5 cm high, up to 2.5 cm dbh/0.01 ha,
HDBHO = hardwood stems >30.5 cm high, up to 2.5 cm dbh/0.01 ha,
EDBH1 = evergreen saplings 2.6-9.9 cm dbh/0.01 ha,
HDBH1 = hardwood saplings 2.6-9.9 cm dbh/0.01 ha,
MINL = lower percent minimum understory,
MINU = upper percent minimum understory,
MAXL = lower percent maximum understory,
GC1 = percent ground cover in annuals,

GC2 = percent ground cover in perennials,
GC3 = percent bare ground (leaves, duff and rock).

Hare tracks intersecting the transect line were totalled and snow depth measured for each 50 m section after each fresh snowfall (Hartmann 1960, Brocke 1975). Problems of high winds drifting fresh snow, and the change from snow to sleet along the altitudinal gradient eliminated many observation days. If any sections of a transect line were not trackable the count for the whole line was not used.

Track counts were used as indices of hare cover preference because they can be measured easily by one person, provided for analysis by habitat, and are good for extensive studies where only relative population levels are needed. Tracks provide an index to the average number of hare using an area part of the time or as part of their home range (Adams 1959, Hartman 1960).

Statistical Model

Ordinary Least Squares

Multivariate ordinary least squares (OLS) regression techniques were used to determine the relationships between hare activity as a dependent variable and weather and habitat measures as independent variables.

The hypothesized relationship was assumed to be linear and of the form:

$$Y_i = \beta_0 + \beta_1 X_{i1} + \ldots\ldots + \beta_k X_{ik} + \epsilon_i \tag{1}$$

where Y_i = the i^{th} value of the entire set of n observations on the dependent variable Y;

X_{ij} = the i^{th} value of the j^{th} independent variable X_j, where j ranges from 1 to k;

Table 1. Dominant species of forest layers and corresponding forest classification system (MacConnell 1975) for zones 1 and 2.

Research areas	Forest[1] types	Tree[2] >10 cm dbh	Saplings 7.5-10 cm dbh	Shrubs up to 7.5 cm dbh
		Zone 1		
0	HS3A SH3A	Bi H Be	Wh Be M	L Wh Be
3	S3A SH3A	H M	S H	H S
4	H3A SH2A	O H	Wh M Be	L Be Wh
8	SH2A HS3A	H M Wp	M	Bl M L H
9	HS3A	M H Bi	Be H	L Wo H M
		Zone 2		
1	SH2A HS3A SH3A	H M S	M H	L Y M
2	SH2A SH3A	Wp S M	M Wp	Sb M S
5	S3A SH3A HS3A	S	M S	M S Bl
6	HS3A HS2A H2A	M Bi H	Bi S M	M S
7	S3A SH2A SH3A	S	S F	S Bl M F

---

[1] Type: H = hardwood and S = softwood, 80% stands; mixed HS = hardwood and SH = softwood predominating
Height: 2= 6.4-12.4 m; 3= 12.5-18.6 m
Crown closure: A= 81-100%; B= 30-80%

[2] H=hemlock, M=maple, F=fir, S=spruce, Bi=birch, O=oak, Be=beech, Wp=white pine, Wh=witch hazel, L=laurel, Bl=blueberry, Wo=witch hobble, Sb=steeplebush, Y=yew.

β_j = the j^{th} unknown parameter to be estimated;

β_o = a constant term;

ε_i = the i^{th} value of the set of n random disturbances about the mean of Y.

Equation (1) can be conveniently expressed in matrix notation as

$$\underline{Y} = X\underline{\beta} + \underline{\varepsilon} \qquad (2)$$

where $\underline{Y}$ = an n x 1 observation vector;

X = an n x k matrix of independent variables;

$\underline{\beta}$ = a k x 1 parameter vector on X;

$\underline{\varepsilon}$ = an n x 1 vector of error terms.

Assumptions of the model are that X is of rank k and that each ε_i is normally and identically distributed, independent of the other disturbance terms, and has mean zero and constant variance σ^2.

Violation of any of these assumptions will render OLS estimation inadequate. Specifically, difficulty with respect to the rank condition of the X matrix, i.e., multicollinearity, requires the implementation of some "treatment." Likewise problems with respect to the error term, e.g., heteroscedasticity or autocorrelation, require some manipulative corrective measure to the data before OLS can be applied.

Pooling Data

A very real problem when dealing with cross-section data and model specification in this case is the matter of organizing the data between the two zones for estimation purposes. That is, the model for each zone relating hare activity to weather and habitat measures can be expressed generally as in equation (2), and the question revolves around the manner of implementing the entire set of data from both zones to get the most efficient parameter estimates.

Let equation (2) be rewritten to represent zone 1 as

$$\underline{Y}_i = X_1\underline{\beta}_1 + \underline{\varepsilon}_1 \qquad (3)$$

where equation (3) is identical to equation (2) except that the subscript 1 relates to zone 1 information. Correspondingly, the model representing zone 2 is

$$\underline{Y}_2 = X_2\underline{\beta}_2 + \underline{\varepsilon}_2. \qquad (4)$$

Estimating the model for zone 1 and zone 2 individually by OLS amounts to the following formulation:

$$\begin{bmatrix} \underline{Y}_1 \\ \cdot \\ \cdot \\ \cdot \\ \underline{Y}_2 \end{bmatrix} = \begin{bmatrix} X_1 & \cdot & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & \cdot & X_2 \end{bmatrix} \begin{bmatrix} \underline{\beta}_1 \\ \cdot \\ \cdot \\ \cdot \\ \underline{\beta}_2 \end{bmatrix} + \begin{bmatrix} \underline{\varepsilon}_1 \\ \cdot \\ \cdot \\ \cdot \\ \underline{\varepsilon}_2 \end{bmatrix} \qquad (5)$$

A most important feature of this model is that arranging the data in this fashion does not restrict the parameters of the independent variables in zone 1 to be equal to those in zone 2, i.e., there are 2k parameters to be estimated in the unrestricted model represented by equation (5).

The inclination of many researchers in such a situation is to "stack" equations (3) and (4) as:

$$\begin{bmatrix} \underline{Y}_1 \\ \cdot \\ \cdot \\ \cdot \\ \underline{Y}_2 \end{bmatrix} = \begin{bmatrix} X_1 \\ \cdot \\ \cdot \\ \cdot \\ X_2 \end{bmatrix} \underline{\beta} + \begin{bmatrix} \underline{\varepsilon}_1 \\ \cdot \\ \cdot \\ \cdot \\ \underline{\varepsilon}_2 \end{bmatrix} \qquad (6)$$

Notice that estimation of this model imposes severe resrictions upon the two parameter vectors of equations (3) and (4), i.e., $\underline{\beta}_1 = \underline{\beta}_2 = \underline{\beta}$. Specifically, the implication is that any particular parameter β_j in zone 1 is equal to the corresponding β_j in zone 2. It is suggesed that, rather than estimating only the stacked model of equation (6) and naively imposing severe restrictions on the parameter space, alternative model specifications ought to be tested against each other and one judged more appropriate than another on the basis of some statistical criterion. One such criterion is the classical F-test (Fisher 1970).

Briefly, the idea is to calculate the residual sum of squares of the unrestricted model (RSS_U) represented by equation (5) and make comparisons with the residual sum of squares of the restricted model (RSS_R) in equation (6). The format for making these comparisons is:

$$F = \frac{(RSS_R - RSS_U) \;/\; (DF_R - DF_U)}{RSS_U \;/\; DF_U}\,, \qquad (7)$$

which is distributed as central F (centrality parameter equal to zero) with (DF_R-DF_U) and DF_U degrees of freedom for the numerator and denominator, respectively. Notice, furthermore, that DF_R and DF_U are the degrees of freedom associated with the restricted and unrestricted models, respectively.

Under the null hypothesis that $\underline{\beta}_1=\underline{\beta}_2=\underline{\beta}$, i.e., that the restrictions suggested by equation (6) hold, versus the alternate hypothesis that $\underline{\beta}_1 \neq \underline{\beta}_2$, i.e., that the restrictions do not hold, equation (7) has particular appeal. Simply stated, if RSS_R and RSS_U are "close" to each other, the implication is that the restrictions are not in conflict with the sample data. This is reflected in a small calculated F-statistic relative to a critical F such that the null hypothesis cannot be rejected. If, on the other hand, RSS_R diverges greatly from RSS_U, the calculated F-statistic will exceed the critical F and the null hypothesis will be rejected, implying that the restrictions are in conflict with the sample data.

Seemingly Unrelated Regression

Once either the stacked or unstacked model has been selected as the appropriate specification, an important issue revolves around whether or not the OLS procedure used for the estimation of the selected model leads to the most efficient parameter estimates. That is, even though 1) the system has been purged of any autocorrelation or heterscedasticity relating to the error structure and 2) possible restrictions relating to the parameters have been tested, additional information may still be gleaned from the estimated error vectors $\underline{e}_1$ and $\underline{e}_2$. In fact, up to now, the assumptions relating to the error terms of either model (5) or model (6) have been very restrictive in the sense that they do not allow for mutual correlation between $\underline{e}_1$ and $\underline{e}_2$. Testing whether or not the error vectors of the selected model (5) or (6) above are actually unrelated or only seemingly unrelated involves a generalized least squares procedure (Zellner 1962). Basically, testing for mutual correlation involves comparing the estimate of the variance of the selected model (5) or (6) above (call this estimate $\hat{\sigma}^2_{OLS}$) with the estimate of the variance of that same model cast in a generalized least squares or seemingly unrelated regression framework (call this estimate $\hat{\sigma}^2_{SUR}$). The hypothesis to be tested is one of homogeneity of variance with the null hypotheis being $\hat{\sigma}^2_{OLS} = \hat{\sigma}^2_{SUR}$ and the alternate hypotheis being $\hat{\sigma}^2_{OLS} \geq \hat{\sigma}^2_{SUR}$. The appropriate test statistic is

$$F = \hat{\sigma}^2_{OLS}/\hat{\sigma}^2_{SUR}$$

If $\hat{\sigma}^2_{OLS}$ is much larger than $\hat{\sigma}^2_{SUR}$, the null hypothesis of no mutual correlation must be rejected.

The appeal of the seemingly unrelated regression approach is that the off-diagonal elements of the variance-covariance matrix of the error term are not restricted to zero (as in the ordinary least squares case) due to possible mutual correlation. Through the generalized least squares algorithm, the degree of mutual correlation in the error structure is analyzed. If there exists little or no mutual correlation, the zero restrictions on the off-diagonals hold, and $\hat{\sigma}^2_{SUR}$ approaches $\hat{\sigma}^2_{OLS}$. On the other hand, the existence of mutual correlation in the error vectors implies the admissibility of additional information about the system which in turn implies that $\hat{\sigma}^2_{SUR} < \hat{\sigma}^2_{OLS}$ and allows for more efficient parameter estimates.

Principal Components

Collinearity among the independent variables can be detected by observing rather high pairwise correlations between explanatory variables and also by performing auxiliary regressions of individual independent variables on the remaining set. This latter test is suggested by Farrar and Glauber (1967).

The way to deal with multicollinearity is to introduce additional sample information to hopefully increase the selective variation among the independent variables. Such information is normally added by way of restrictions on the parameters suggested by theory. These restrictions may take the form of exact linear restrictions (Goldberger 1964: 256-8), inequality restrictions (Judge and Takayama 1966), and stochastic restrictions (Theil and Goldberger 1961).

In the absence of any theoretical basis for admitting restrictions on the parameters, an alternative is to place restrictions on the independent variables themselves. This can be accomplished by transforming the original variables into artificial constructs that are orthogonal to each other and then retaining certain of these constructs in a regression model on the basis of their contribution to variability in the original data, while eliminating--placing zero restrictions on--those constructs that contribute little or nothing to the variability in the original data. This is precisely the focus of principal components.

In principal components regression, a transformed variable is determined to be important and included or unimportant and excluded in the regression model depending upon the size of the characteristic root (eigenvalue) associated with its corresponding characteristic vector (eigenvector) (Massy 1965), the statistical significance of its regression coefficient (Mittelhammer and Baritelle 1977), or some combination of eigenvalue size and correlation with the dependent variable (Johnson et al. 1973).

A complication results with respect to the optimal number of components to delete. The tendency traditionally has been to delete components asociated with small eigenvalues, e.g., less than one. The limitation of this approach is that components with small eigenvalues may be correlated very highly with the dependent variable. Thus, a structural norm which simultaneously considers the amount of variability accounted for by a particular component and its correlation with the dependent variable has greater appeal. A particular norm which accounts for these two measures is the F-test described in equation (7). Components can be sequentially deleted until a new restriction, i.e., the deletion of an additional component, causes no improvement with respect to the fit of the equation. Finally, once the "optimal" number of components has been deleted, the principal component estimators can easily be transformed to estimators on the original independent variables (Johnson et al. 1973).

RESULTS AND DISCUSSION

OLS regression models were estimated individually for zone 1 (n=384) and zone 2 (n=480) in the spirit of equation (5) and with the zones stacked (n=864) as suggested by equation (6). Preliminary to performing these regressions, any problems with respect to heteroscedasticity among the error variances of the individual areas were corrected. The model specifications were tested using equation (7) to determine if the parameter restrictions held. The F-values were significant using the central F-test. This separation was consistent with development of these ecological zones and indicates that there were major habitat differences.

Seemingly unrelated regression (SUR) was done on the unstacked data and the possibility of mutual correlation explored. The disturbances in the two equations were found to be not mutually correlated, and the SUR parameters estimators were the same as the OLS estimators. The above tests showed that both the set of explanatory variables and disturbances between zones were not correlated, and there was no justification for combining the data.

Multicollinearity among the explanatory variables was indicated by significant relationships in the simple correlations and auxilliary regressions. Almost perfect collinearity existed between each of the three ground cover measurements (GC1, GC2, AND GC3) and the remaining variables. This was expected, as ground cover was a function of the amount of light reaching the forest floor which, in turn, was determined by canopy closure and understory. Basal area (BA), a measure of canopy closure, was also collinear with the rest of the variables. Furthermore, collinearity among the independent variables was confirmed in that the OLS regressions for each zone had high standard errors resulting in non-significant t-statistics.

Principal components regression (PCR) was done on each zone. Equation (7) was used as the deletion criterium with one component deleted from zone 1 and four from zone 2. Because information was removed from the models, the t-tests were recognized only as indicators of more precise estimators and suggest variables that may be most important habitat descriptors (Freund 1974). Final PCR model coefficients and significance tests appear in tables 2 and 3. The fact that zone 1 was an area of transition between the Connecticut River Valley lowlands and upland Berkshire Mountains indicated that it would be difficult to find common parameters within this zone's heterogeniety.

The final model for zone 1 had eleven significant effects while zone 2 had eight. Three variates of major importance were retained with the same sign in both models. Species richness (RICH), indicating open areas, and basal area (BA), or canopy closure, had negative effects on hare abundance while hardwood shrub frequency (HDBHO) had a positive effect. Four additional variable effects were significant in both zones but carried opposite signs: number of evergreen (EVER) and hardwood (HARD) trees, number of evergreen saplings (EDBH1), and upper percent winter understory (MINU). Sample data were carefully examined for the possibility that the signs changed in response to a particular sensitivity in habitat measurements. The number of hardwood trees appears to have a sample frequency that could explain the change in signs (fig. 2), but because zone 1 already had more hardwood trees, the only interpretation was that increasing numbers of hardwood trees in zone 1 is related to increased hare activity, while in zone 2 the inverse held. The histogram in figure 3 demonstrates the relative frequencies for evergreen trees was similar in both zones, as they were for EDBH1 and MINU, so the same effects were expected but not found.

One hypothesis for the different effects between zones is that the low hare track count of 298 for zone 1, compared with 2226 tracks for zone 2, had low information content for selection of variable effects and the quality of the parameter estimates were questionable. When EVER and HARD were plotted on a three dimensional graph (fig. 4) the same frequency distributions were seen but in addition the low track count values of zone 1 were evident.

There are possible explanations for the different variable effects between zones based on

Table 2. Principal components regression model of the relationship between hare activity and selection of habitat in zone 1.

Variable[1] Names	Estimated coefficients	T- ratio[2]
RICH	-0.115	-1.933*
SNOW	0.010	2.292**
EVER	0.340	7.238**
HARD	0.088	2.347**
BA	-0.064	-4.796**
SHRUB	-0.001	-0.321
EDBH0	-0.009	-1.745*
EDBH1	-0.028	-2.471**
HDBH0	0.003	3.189**
HDBH1	-0.002	-0.419
MINL	0.014	3.056**
MINU	-0.016	-2.382**
MAXL	-0.012	-2.472**
GC1	0.001	0.101
GC2	-0.006	-0.679
GC3	-0.001	-0.103
Intercept	1.459	

[1] see text for variable description

[2] ** P<0.01, * P<0.05

Table 3. Principal components regression model of the relationship between hare activity and habitat component selection in zone 2.

Variable[1] Names	Estimated coefficients	T- ratio[2]
RICH	-0.148	-2.337**
SNOW	-0.013	-1.523
EVER	-0.120	-2.240**
HARD	-0.315	-3.732**
BA	-0.040	-2.816**
SHRUB	0.008	0.512
EDBH0	-0.006	-0.968
EDBH1	0.066	3.166**
HDBH0	0.010	2.761**
HDBH1	0.096	5.430**
MINL	-0.012	-1.074
MINU	0.051	2.747**
MAXL	0.007	0.690
GC1	-0.019	-1.294
GC2	-0.020	-1.233
GC3	0.016	1.698*
Intercept	3.181	

[1] see text for variable description

[2] ** P<0.01, * P<0.05

field observation. For example, median snow depths were the same for both zones while the maximum depth was 41 cm deeper on zone 2. Heavier snows in zone 2 had a greater immediate effect on the habitat. Accumulation of snow on tree branches and crowns bent them down within reach for browsing, and often broke them off entirely providing tips, and buds for food on top of the snow. Shrubs and saplings became completely covered with snow in some storms and hare burrowed under them and used these areas for food and shelter. Snowfalls in zone 1 were lighter and melted faster with less accumulation, due to more mature trees and denser canopy intercepting the snow, preventing most tree damage. This relationship between snow and vegetation in the two zones explained the hares' selection of different components in the sapling (EDBH1 and HDBH1) and density (MINL, MINU and MAXL) classes.

Additional hypotheses could be suggested pertaining to differences between the models for each zone, e.g., response to different species of vegetation, interspecific competition between hare and white-tailed deer (_Odocoileus virginianus_), and the predator-food complex, but the important point has already surfaced. If the parameter estimates of these models had been restricted by pooling the two data sets, none of these differences between zones and ultimately hare habitat would have been qualified. Opposite effects for the same variable between zones would have eliminated detection of some significant habitat descriptors and given poor quality estimates for others. This problem has severe limitations when these data are being used as a basis for designing and implementing management plans. Too often in wildlife research, extensive habitat management plans are based on local intensive studies. Wildlife managers cannot afford to have unrealized negative effects of habitat manipulation surface, by either short-term

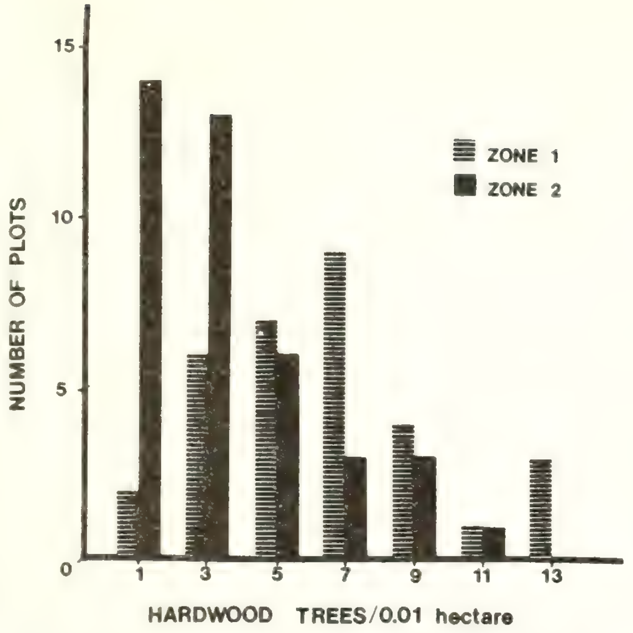

Figure 2. Comparison of frequency distributions of hardwood trees > 10 cm dbh for both zones.

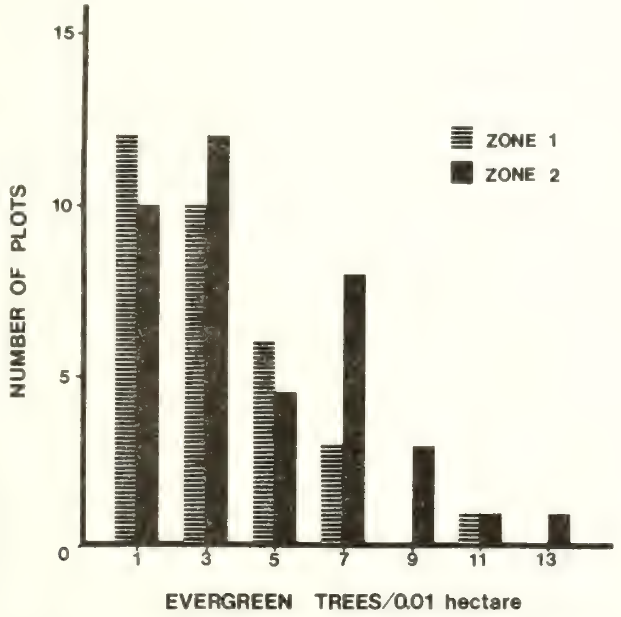

Figure 3. Comparison of frequency distributions between evergreen trees > 10 cm dbh for both zones.

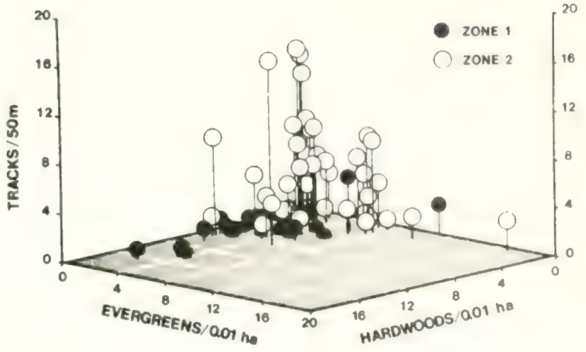

Figure 4. Three dimensional plot of the relationship between hare track counts and number of evergreen and hardwood trees > 10 cm dbh for both zones.

losses of the wildlife in that habitat or long term destruction that will discourage potential immigrating populations.

More specifically, the two zones in this study should be managed differently assuming the parameter estimates are valid. Zone 2 model estimates agreed with our observations of hare activity over the past 2 years, and were consistent with earlier studies in good hare range. The predominately hardwood habitat in zone 1 has only been studied quantitatively recently, and not in areas with the same species composition as this study. Sheldon (1957) stated that northen hardwood-laurel, and hemlock-laurel habitats in zone 1 were the most widespread and important in Massachusetts yet in this study they have the lowest populations. The zone 1 model should be tested with more data to see if the parameter effects hold or will move closer to the other zone model.

ACKNOWLEDGMENTS

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DISCUSSION

GEORGE BURGOYNE, JR.: Would you care to comment on the justification for treating a large number of observations collected at five sites in two regions as completely independent observations. The fact that only ten sites were used would be expected to yield more homogenous results than if the same number of transects were really located at random. It is difficult to believe that two 50 meter transects adjacently located are as independent as two 50 meter transects independently, randomly located.

KATHRYN CONVERSE: Vegetation frequency, composition, and structure was heterogenous along the ten transect lines. Any problems of the dependence with repeated observations was corrected by orthogonalizing variables using Principle Components. Certainly adjacent 50 m transects are less independent than random 50 m transects, but they did allow for repeated detailed observations of changing hare activity and habitat use with varying weather conditions as the winter progressed. Intensive vegetation measurements and winter tracking over 960 randomly located transects would have been logistically impossible for one person.

KEN MORRISON: Being familiar with animal tracking, I have a gut feeling that the error in measurement increases with increasing activity levels, suggesting that a transformation, perhaps log, would be appropriate? Is it possible that this could have been the case in your study?

KATHRYN CONVERSE: Indeed, a log transformation may be appropriate. We failed to test among competing functional specifications for our model. We merely assumed linear relationships.

KEN MORRISON: The number of crossings will be a function of time since the last snowfall. When you were sampling, is it possible that you consistently sampled one area before the other, thereby creating a biased difference between the two?

KATHRYN CONVERSE: Two sets of five study areas that were a mixture from both zones were tracked in alternating order after each snowfall. I think this would eliminate any bias between zones.

DOUGLAS INKLEY: Do you think that snow depth may have had an effect on hare mobility, and therefore different regional track counts may have been due to both population differences and the effect of snow depth on mobility?

KATHRYN CONVERSE: Regional hare activity was definitely influenced by snow depth, consistency, and accumulation. Inclusion of these snow conditions as variables in this model helped to explain changing food and cover availability by habitat types throughout the winter months.

MARTIN RAPHAEL: How do you derive the individual parameter estimators, i.e., how do you get unique estimators using principal components?

BERNARD MORZUCH: The process is very mechanical and straightforward (See Morzuch, B.J. 1981. Principal components and the problem of multicollinearity. Journal of the Northeastern Agriculture Economics Council. In press.).

LESLIE MARCUS: The "seemingly unrelated regression" application to the two zone hare data seems inappropriate. Since the individual plots between zones (C_{1i} and C_{2i}) are not "contemporaneous elements" (Zellner, A. 1963. Estimators for seemingly unrelated regression equations: some exact finite sample results. American Statistical Association Journal 57:350-367.), there is no reason to relate them. The value of C_1C_2 calculated to estimate σ_{12} depends on the permutation of the M_1 and M_2 observations, and over permutations $E(C_1C_2) = 0$. Since it might happen that $M_1 \neq M_2$ depending on sampling design etc., this is an unnecessary application of the interesting idea. Note if the sampling sites had been sampled in the same order in the two zones or at similar times of the day, this might be a useful test. The way Ms. Converse explained the data collection it does not seem appropriate.

BERNARD MORZUCH: As background to answering this question, two entirely different zones (within which five areas were identifed, with eight plots per area) were delineated on the basis of vegetation and elevation. There was no attempt to match a particular plot in zone 1 against any one plot in zone 2. Alternatively, performing all possible permutations to find one ordering that provided the highest degree of mutual correlation was not the central theme of this analysis.

Relative to the question, who is to say that ordering the cross sections in zones 1 and 2 in a particular fashion to make certain that we have a matching of contemporaneous elements is the one correct ordering so as to make use of Zellner's framework. Given the heterogeneous nature of plots between zones and the lack of theory to suggest a proper matching, alternative orderings, i.e., random or otherwise, are appropriate.

The purpose of the study was to establish a functional relationship between hare distribution and habitat variables. The resulting estimators of the pooled model have, at least, nice asymptotic properties. Therefore, any additional testing of the restrictive assumptions of the OLS model that might lead to greater efficiencies in the estimators would be most welcome. Such is the purpose of testing for mutual correlation in a seemingly unrelated (SUR) framework. Applying SUR in this fashion is, most certainly, appropriate and not an unnecessary application of an interesting idea. Given our ordering of contemporaneous elements, we were unable to conclude the presence of mutual correlation. This is not to say that another ordering would lead to the same conclusions on efficiency grounds. However, consistency and asymptotic unbiasedness of the estimators would remain unaffected under any ordering.

A DISCUSSION OF ROBUST PROCEDURES IN MULTIVARIATE ANALYSIS[1]

Lyman L. McDonald[2]

Abstract.--Robust procedures in multivariate analysis are briefly reviewed. Conjectures are given for applications of existing methods in other areas of multivariate analysis.

Key words: Discriminant analysis; multicollinearity; outliers; principal components; robust procedures.

Upon review of titles of papers to be presented at this meeting, my first reaction was to discuss a combination of three subjects: 1) the danger of "overfitting" multivariate data with descriptive procedures such as principal components, factor analysis and canonical correlation analysis; 2) the ultra-conservative nature of inference procedures in multivariate analysis of variance (MANOVA) and in multivariate regression analysis (i.e., simultaneous regression of several dependent variables on a collection of independent variables); and 3) the need for "robust" analysis procedures in multivariate studies.

The first of my concerns is addressed by Karr and Martin (1981). Their observations reinforce my experiences and I endorse their suggestion that "One possibility might be a table of expected amount of variation accounted for by random number matrices that can be used as a test relative to the amount of variation accounted for in real data." Actually tables of upper percentage points in the null distribution of variance accounted for by random number matrices would be more appropriate for a formal test of hypothesis, but the idea is the same.

The second of my concerns is not of much interest in the papers presented. MANOVA is mentioned rarely and insofar as I am aware, the corresponding simultaneous inference procedures are not strongly recommended.

I emphasize, then, the third topic: a need for robust procedures. This need becomes obvious when reading several of the papers. For example, Williams (1981) correctly pointed out that an important aspect of canonical variates in discriminant analysis is the ecological meaning of the coefficients. However he noted that "Most people who have worked with discriminant analysis have probably seen cases in which positively correlated variates have canonical coefficients with different signs," and quoting from Weiner and Dunn (1966), "For complex structures, magnitudes and even signs of coefficients are dependent on what additional variables are included in the model." In a study of discriminant analysis by use of multiple regression methods, Cavallaro et al. (1981) stated that "Multicollinearity can cause the regression coefficients to be inflated in absolute value or even to have the wrong sign." Smith (1981) in his paper on canonical correlation analysis noted that "Most often coefficients are exceedingly difficult to interpret, if not meaningless (Cassie and Michael 1968). . . ." Also, ". . .Cassie (1969) found that adding and subtracting variables at random 'capriciously' changed the values of the corresponding canonical coefficients." Harner and Whitmore (1981) stated that "Outliers in multivariate data can have pronounced effects on the interpretations and conclusions of statistical analyses."

With the exception of Harner and Whitmore (1981) and Cavallaro et al. (1981), little information has been given in these proceedings to help the reader understand and solve these problems when they arise in a particular application. Instead, the reader is warned that problems may exist and in some cases analysis procedures for detection of the need for more robust methods have been given (e.g., data splitting). However, alternative methods have not always been given if unstable results occur in the analysis of a particular data set.

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[1] Paper presented at The use of multivariate statistics in studies of wildlife habitat: a workshop, April 23-25, 1980, Burlington Vt.

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There appear to be two basic problems and hence at least two approaches to "robust" multivariate analysis procedures: 1) elimination (or reduction) of multicollinearity before inversion of a variance-covariance type matrix--or equivalently, improved estimation of the inverse of a variance-covariance matrix; and 2) robust estimation of parameters by some procedure for outright trimming of "outliers" or for reduction of the influence of outliers.

Consider first the problem of reducing effects of multicollinearity on multivariate procedures. Most multivariate methods, except for descriptive procedures such as principal components and factor analysis, involve the inverse of a matrix, $\underline{S}$, of sums of squares and cross-products. Correlation matrices, variance-covariance matrices, etc., are all special cases. Letting $\lambda_i, i=1,\ldots,p$, denote the characteristic roots of a (p x p) nonsingular matrix $\underline{S}$, one can write

$$\underline{S}^{-1} = \sum_{i=1}^{p} (1/\lambda_i)\, \underline{a}_i \underline{a}_i' \qquad (1)$$

where $\underline{a}_i$ denotes the corresponding normalized characteristic vectors. If some of the variables used to compute $\underline{S}$ are strongly intercorrelated (i.e., there is multicollinearity) then some of the characteristic roots will be "small" and the matrix $\underline{S}$ is said to be ill-conditioned. Clearly from Eq.(1) division by small values is involved and the inverse of $\underline{S}$ will be unstable in such cases. Consider the obvious effect in regression analysis $[\hat{\beta} = \underline{S}^{-1}\underline{X}'\underline{Y}]$, discriminant functions $[D(\underline{X}) = (\underline{\bar{X}}_1-\underline{\bar{X}}_2)'\underline{S}^{-1}\underline{X}]$, Mahalanobis' distance $[D^2 = (\underline{\bar{X}}_1-\underline{\bar{X}}_2)'\underline{S}^{-1}(\underline{\bar{X}}_1-\underline{\bar{X}}_2)]$ and canonical variables and correlations [characteristic roots and vectors of $\underline{S}_{11}^{-1}\underline{S}_{12}\underline{S}_{22}^{-1}\underline{S}_{21}$ and $\underline{S}_{22}^{-1}\underline{S}_{21}\underline{S}_{11}^{-1}\underline{S}_{12}$] where standard notation is used. The regression coefficients, discriminant coefficients, . . ., will be impossible to interpret if the problem is severe.

Regression analysis has, of course, received the most attention under two general approaches. First, regression on the first few principal components (say q with q < p) eliminating those corresponding to small characteristic roots. The results are obvious in that the reduced coefficient matrix of the normal equations is diagonal and the regression coefficients are

$$\underline{\beta}^* = (\mathrm{diag}\ (\lambda_1,\ldots,\lambda_q))^{-1} \begin{bmatrix} \underline{a}_1' \\ \cdot \\ \cdot \\ \cdot \\ \underline{a}_q' \end{bmatrix} \underline{X}'\underline{Y}\ .$$

Increased stability can be expected with usually only a minor increase in bias. Sczerzenie (1981), in his paper on analysis of deer harvest-land use relationships, correctly noted that the procedure will often reduce the variance of the estimators. Converse and Morzuch (1981) noted that the procedure will decrease the effect of multicollinearity among independent variables. For further details on this procedure, the interested reader is referred to Sczerzenie (1981) and Converse and Morzuch (1981) and their cited references.

Use of principal components to reduce the effect of multicollinearity in multivariate procedures other than regression analysis has been proposed but not studied (insofar as I am aware). The approach is to transform all data to the first few principal components before starting the analysis. Variables are then uncorrelated and only diagonal matrices need to be inverted. For example, Fisher's linear discriminant function

$$D(\underline{X}) = [(\underline{\bar{X}}_1 - \underline{\bar{X}}_2)'\underline{S}^{-1}]\underline{X}$$

would be replaced by

$$D^*(\underline{X}) = [(\underline{\bar{X}}_1 - \underline{\bar{X}}_2)'\underline{A}')(\underline{A}\underline{S}\underline{A}')^{-1}\underline{A}]\underline{X} \text{ where}$$

$\underline{A}_{qxp}\underline{X}_{px1}$ represents the transformation of all data to the "first" q principal components, q < p. Hopefully, the loadings in $D^*(\underline{X})$ will be more stable and easier to interpret than in the original function without sacrificing the discriminating ability. Similar adjustments can be made in canonical variate analysis and other multivariate procedures.

The second approach to solving the problem of multicollinearity in regression analysis is by ridge regression or biased-regression, first developed by Hoerl and Kennard (1970). Cavallaro et al. (1981) gave an excellent application of this procedure in their use of multiple regression techniques for discriminant analysis. The basic idea is to allow a certain bias in the regression coefficient by adding a constant k to the diagonal of the coefficient matrix of the normal equations before inverting, i.e.,

$$\hat{\underline{\beta}} = (\underline{S}+k\underline{I})^{-1}\underline{X}'\underline{Y}.$$

This operation will add the constant k to all characteristic roots of $\underline{S}$ and hence

$$(\underline{S}+k\underline{I})^{-1} = \sum_{i=1}^{k} [1/(\lambda_i+k)]\underline{a}_i\underline{a}_i'\ .$$

Ridge regression can be viewed as a special application of a much broader problem, namely improved estimation of the inverse of a variance-covariance matirx, e.g., Efron and Morris (1976). In general, small characteristic roots of $\underline{S}$ are underestimates of the corresponding population values and large roots are overestimates. Efron and Morris sought to improve $\underline{S}^{-1}$ by shrinking all roots toward a common value. The ridge-adjusted estimate, $(\underline{S}+k\underline{I})^{-1}$, works by increasing all roots by a constant amount, k. Thus the ill-conditioning effect of underestimating small roots is countered without having much influence on the larger roots. I will refer to estimates of $\underline{\Sigma}^{-1}$ based on adjusted roots of $\underline{S}$ as simply ridge-adjusted estimators.

I am aware of two investigations into the use of ridge-adjusted estimates of $\underline{\Sigma}^{-1}$ in linear discriminant analysis, i.e.,

$$D^*(\underline{X}) = [(\underline{\overline{X}}_1 - \underline{\overline{X}}_2)'(\underline{S} + k\underline{I})^{-1}]\underline{X}.$$

The first by DiPillo (1976) showed that when the variance-covariance matrices are ill-conditioned, improvements can be made in the probability of correct classification. In an independent investigation, Smidt and McDonald (1976) found no improvement in classification rate but obtained increased stability in estimates of coefficients of discriminant functions.

I am not aware of research of this type into the study of canonical correlation analysis and other procedures but would conjecture that similar improvements can be made by using ridge-adjusted estimators of the inverse of variance-covariance matrices.

The second area of development of robust multivariate analysis procedures is in the reduction of the effect of outliers on resulting analyses. It is well known that outliers in multidimensional studies are very difficult to detect, and if undetected can have a pronounced effect on the analysis. Harner and Whitmore (1981) developed a method for building robust discriminant models. In general, they found that in the presence of outliers robust models performed much better than Fisher's discriminant model. With such an improvement in discriminant analysis it is almost a certainty that other multivariate procedures will perform better if the influence of outliers is reduced. Guarding against the adverse effects of outliers should be a goal in every data analysis. The interested reader is referred to cited references in Harner and Whitmore's excellent paper for further work in this area.

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